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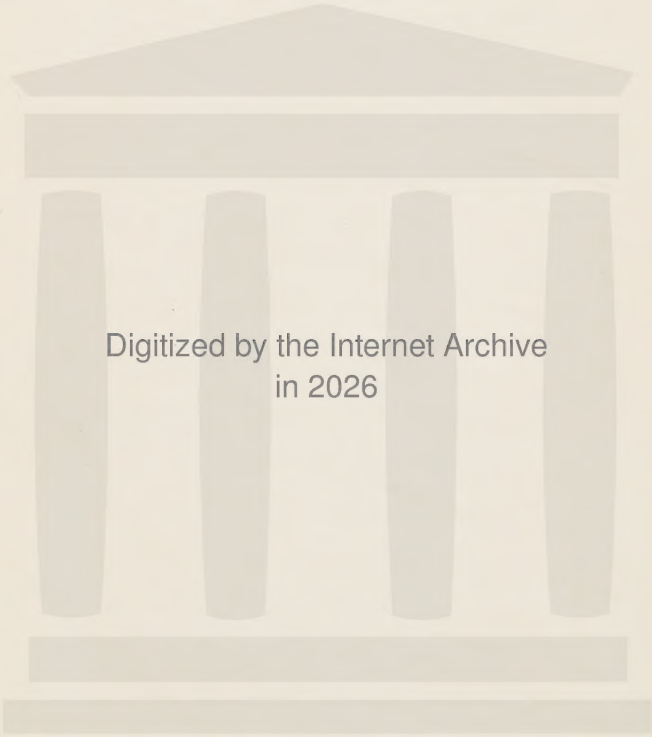
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A TEXTBOOK OF BOTANY

FOR

COLLEGES AND UNIVERSITIES

BY MEMBERS OF THE BOTANICAL STAFF OF
THE UNIVERSITY OF CHICAGO

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W. P. 5

PREFACE

THE study of plants has assumed so many points of view that every laboratory has developed its own method of undergraduate instruction. No laboratory attempts to include all the phases of work that may be regarded as belonging to botany; and therefore each one selects the material and the point of view that seem to it to be the most appropriate for its own purpose. During the last ten years the Hull Botanical Laboratory at the University of Chicago has been developing its undergraduate instruction in botany to meet its own needs. Freed from the necessity of laying special stress upon the economic aspects of the subject, and compelled to prepare students for investigation, it seemed clear that its selection must be the fundamental facts and principles of the science. Its endeavor has been to help the student to build up a coherent and substantial body of knowledge, and to develop an attitude of mind that will enable him to grapple with any botanical situation, whether it be teaching or investigation. It has been thought useful to present this point of view in the present volume. The material of course is common to all laboratories, but its selection, its organization, and its presentation bear the marks of individual judgment.

The three parts of the book represent the three general divisions of the subject as organized at the Hull Botanical Laboratory. They are felt to be the fundamental divisions which should underlie the work of most subdivisions of botanical investigation. For example, a study of the very important subject of plant pathology must presuppose the fundamentals of morphology and physiology; paleobotany is, in part, the application of morphology and ecology to fossil plants; and scientific plant breeding rests upon the foundations laid by morphology, physiology, and ecology. In our selection for undergraduate instruction, therefore, we believe that there has been in-

cluded the essential foundation for most of the varied work that is included to-day under botany.

We recognize that the presentation of the three great subjects here included is very compact, but the book is not intended for reading and recitation. The teacher is expected to use it for suggestive material and for its organization; the student is expected to use it in relating his observations to one another and to the general points of view that the book seeks to develop. There is a continuity of presentation in each part, so that random selection may miss the largest meaning. For example, in the part on morphology, the thread upon which the facts are strung is the evolution of the plant kingdom, and each plant introduced has its peculiar application in illustrating some phase of this evolution. When certain groups are selected for laboratory study, therefore, the intervening text should be read.

It is important to call attention to the fact that the book has been prepared for the use of undergraduate students. It does not represent our conception of graduate work, which should include much that is omitted here. For example, the graduate student should be introduced to the original sources of information, which would involve an extensive citation of literature far beyond the needs of the undergraduate. Still less has this book been written for our professional colleagues, who will notice what they may regard as glaring omissions. Such omissions must be taken to express a deliberate judgment as to what may be omitted with the least damage to the undergraduate student. The motive is to develop certain general conceptions that are felt to be fundamental, rather than to present an encyclopedic collection of facts. This purpose has demanded occasionally also a greater apparent rigidity of form in general statements than is absolutely consistent with all the facts; but it was a choice between a clear and important conception for one with no perspective and a contradiction of large truths by isolated facts, resulting in confusion. For the same reasons, the extensive terminology of the subject has been kept in the background as much as possible. Definitions usually are made an incident to the necessary introduction of terms. It is assumed that in so far as the definite application of a term may not seem clear, the student will find a compact definition in the current dictionaries.

For the benefit of the teacher and of our professional colleagues, it should be stated that much attention has been given to the avoidance of any phraseology that might involve a teleological implication. It has not been possible to avoid such phrases in all cases without introducing clumsiness of expression or breaking the continuity of some important series of structures or events. It should be kept in mind, therefore, that all teleological implications of language that remain are disavowed.

It seems hardly necessary to say that most of the material presented in the book has been worked over by classes repeatedly. Some new matter has been developed incidentally in all the parts in connection with ordinary laboratory and field work; and especially in Part III have many scattered observations and some new points of view been included. There has been no intention to include any formal contribution, but merely to present in general outline some of the material worked over by undergraduates, some of the results of investigation already published in contributions from the laboratory, and some observations and conclusions that hardly seemed to justify separate publication. Provision has been made for students with more interest or more time than usual to get a somewhat larger view, by including in smaller type further details of structure, additional illustrative material, and suggestive theories. Most of the illustrations are original, in the sense that they have been prepared especially for this book or have appeared in our own contributions. Those that have been copied or adapted are credited; the former usually being indicated by "from," the latter by "after."

The three authors are individually responsible only for their own parts, and, while they had the advantage of mutual criticism, it could not be expected that they would agree absolutely at every point. This will explain any lack of harmony that may be discovered in the three parts. A morphologist, a physiologist, and an ecologist look at the same material from different angles, and lay emphasis upon different features; but all their points of view should be included in any general consideration of plants. It is for this reason, also, that the parts contain a certain amount of repetition, which is absolutely necessary when the same structures or functions are being considered from different points of view.

The selection and preparation of the illustrations for Part I were under the efficient direction of Dr. W. J. G. Land, and most of the original drawings of the book were made by Miss Anna Hamilton, an artist to whom great credit is due. We owe certain original illustrations to the cooperation of our colleagues, who are named in connection with the figures; and also some of the drawings in Part III to Miss Anna M. Starr. In addition to the mutual criticism of the authors, Dr. C. J. Chamberlain, Dr. William Crocker, and Mr. George D. Fuller made helpful suggestions in reading the proof. For such errors as remain, after all our efforts to eliminate them, the authors themselves assume full responsibility. In correcting them, we shall welcome the help of the wider circle of users to whom the book now goes.

JOHN M. COULTER.
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PART I — MORPHOLOGY

CHAPTER I — THALLOPHYTES

Introductory. — Thallophytes form the lowest great division of the plant kingdom, the name meaning "thallus plants." A thallus is a plant body in which there is little or no differentiation of vegetative organs. Among the higher plants differentiation results in such distinct vegetative organs as stems and leaves. A thallus body does not distinguish thallophytes absolutely, for some thallophytes have differentiated vegetative bodies, and thallus bodies are found in other groups of plants. However, the greatest display of thallus bodies is found among thallophytes, and the name is reasonably distinctive.

As the thallophytes include the lowest plants, the group is especially interesting as representing the living forms nearest to the beginnings of the plant kingdom. Among these plants the beginnings of structures are found that are observed to become modified in various ways in the higher groups. A fundamental conception of the plant kingdom is that it begins with simple forms and advances gradually to more complex forms, until the highest group of plants is reached. To appreciate this evolution of the plant kingdom it is necessary to study plants in this order, beginning with the thallophytes.

A natural classification of thallophytes, which means a classification based upon relationships, is impossible at present, and any presentation of them must be more or less artificial. Two groups stand out conspicuously, known as *Algae* and *Fungi;* but there are other groups of thallophytes whose relationships are puzzling. Sometimes the latter groups are distributed among algae and fungi, but this is far from satisfactory. In the following presentation the doubtful groups will be kept separate from the true algae and fungi.

1. MYXOMYCETES

General description. — These organisms are commonly known as slime molds or slime fungi. They combine characters of plants and of animals in such a way that opinions differ as to whether they should be

regarded as plants or animals. Those who incline to the view that they are animals use the term *Mycetozoa* (fungus animals) for the group. It should not be surprising to find at the lower confines of the plant and animal kingdoms organisms which do not appear to belong to either.

The slime molds are mostly terrestrial forms, being common in forests on humous soil, decaying wood, fallen leaves, etc., and one of the largest occurs on spent tan bark ("flowers of tan"). The body contains no chlorophyll, and this fact has induced many to regard slime molds as fungi. The absence of chlorophyll means inability to manufacture food, and hence a dependent habit, slime molds being for the most part saprophytes (see p. 61).

Plant body. — The characteristic body is called the *plasmodium*, which is a naked mass of protoplasm (the living substance) with a creeping motion, putting out and withdrawing regions of its body (*pseudopodia*) like a gigantic amoeba (see p. 444). This slimy body is for a time very sensitive to light, in the case of the slime mold of tan, for example, shrinking away from it into the crevices of its substratum. Within the body there are found embedded many nuclei (protoplasmic organs), and streaming movements in the cytoplasm (the general protoplasm) may be observed (fig. 1). The most unplantlike behavior of the plasmodium is its habit of engulfing solid food instead of admitting it in solution, and within the body may be seen engulfed bacteria and other minute organisms. Under certain conditions, the whole plasmodium or parts of it become encysted, the surface becoming hardened and often crusty and inclosing a mass of resting protoplasm of waxlike consistency. These hardened masses are called *sclerotia*, and are wonderfully resistant, being capable of renewing their activity after remaining dry for years.

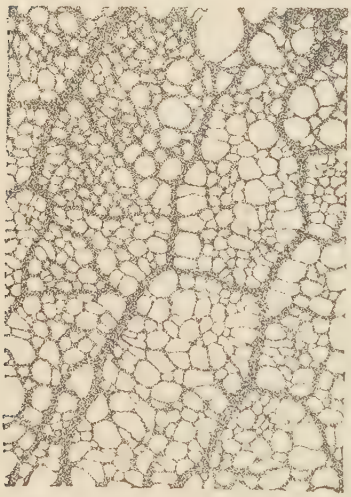


FIG. 1. — A small portion of the plasmodium of a slime mold (*Fuligo*), highly magnified; the cytoplasm is very vacuolate, so that it appears as a network of strands of varying width, in which numerous nuclei may be observed. — Adapted from LISTER.

Reproduction. — At the time of spore-formation, the plasmodium comes to the surface of its substratum, sometimes climbing along various supports, and then locomotion ceases. The whole plasmodium then forms a single stalked *sporangium* (spore case); or it organizes several regions, each of which produces a sporangium, the sporangia often forming a close cluster (fig. 2). In sporangium formation the pulsating advance of the protoplasm has been observed, forming the hollow stalk and finally the terminal spore case, whose wall hardens into a firm sheath. Nothing is left of the unused plasmodium, except a network of tough strands. The spore case is exceedingly variable in form and general appearance, and often within it there is organized a network of tubes known as the *capillitium*. In the meshes of this network countless spores are formed, with cellulose walls, most characteristic reproductive cells of plants. The wall of the spore case dries and ruptures, and the hygroscopic capillitium expands, often carrying up and exposing the spores to dispersal.

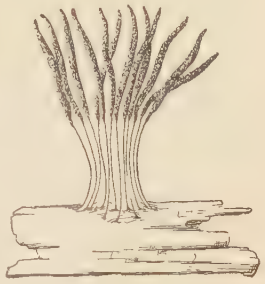


FIG. 2. — A group of sporangia of *Stemonitis*, arising from a plasmodium on a fragment of wood, showing the slender stalks and linear spore cases.

The structure of the sporangium is not always so complicated as the one described, for sometimes there is no capillitium, and sometimes there is no stalk. Even the spore case may be lacking, the spores being cut off from branches sent out from the stalk. A still greater modification in spore formation is exhibited in such forms as the common flowers of tan (*Fuligo*), in which no distinct sporangia are seen, but the whole plasmodium and sometimes several blended plasmodia become transformed into a cushion-like or cakelike mass, known as the *aethalium*. Within the aethalium the spores are found in irregular chambers, which may be taken to represent a confused mass of indefinite and blended sporangia.

Life history. — In following the life history from spore to plasmodium great variations are encountered, for at every stage there is exhibited extreme sensitiveness to external conditions. A representative series of stages is as follows: From the spore wall the amoeboid protoplast escapes and soon develops a single cilium or flagellum, by means of which it moves very actively. This ciliated cell has quite the appearance of certain low animals in structure as well as in movements, and it multiplies freely by division. Eventually the cilium disappears and the cell becomes amoeba-like again, and in this condition it may mul-

tiply indefinitely by division. Finally these amoeboid cells begin to coalesce and a plasmodium is gradually built up (fig. 3). The individual amoeba-like cells that enter into the structure of the plasmodium may lose their identity or not, but their nuclei do not fuse. A plasmodium, therefore, is a mass of coalesced naked cells, each represented in the complex body at least by its nucleus. It would be confusing to indicate the variations that may occur in this life history. It is sufficient to say that the flagellum stage is regularly absent in certain forms, and that the flagellum stage and amoeba stage may encyst repeatedly before the formation of a plasmodium.

FIG. 3. — A small group of amoeboid cells, each containing a distinct nucleus, beginning to coalesce in the formation of a plasmodium. — Adapted from SACHS.

In general it may be said that the structure and behavior of the nutritive body of these organisms would seem to relate them to animals; but that the spore-forming structures are just as distinctly those of plants.

2. SCHIZOPHYTES

The name of the group means "fission plants," referring to the fact that the characteristic cell divisions occur in rapid succession and represent the only method of reproduction. The two divisions of schizophytes are distinguished in general by the presence and absence of chlorophyll, which means that one group comprises independent, food-manufacturing plants, and that the other comprises parasites and saprophytes (see p. 61).

(1) CYANOPHYCEAE

General description. — These are the blue-green algae, as indicated by the name, and very commonly they are presented as one of the groups of algae. This association is made chiefly because of the presence of chlorophyll, but the differences from the true algae are so important that the ability to manufacture food should not outweigh them. A consistent name for the group is *Schizophyceae* (fission algae), but we have retained the name which is in far more common use, and which refers to the most conspicuous feature of the group, namely, the usual presence of a blue pigment (phycocyanin) in addition to the green. This association of chlorophyll (?) and phycocyanin gives to the plants, at least in

mass, a characteristic bluish green color, quite distinct from the yellow-green color of the green algae.[1]

The Cyanophyceae are found everywhere in fresh and salt water; and also on damp soil, rocks, bark, etc. A conspicuous free-floating form gives the characteristic hue to the Red Sea, a fact which indicates that "blue-green" algae may be red. They occur also in the water of hot springs, thriving in a temperature that most other plants could not endure. The sinter deposits which give character and attraction to the craters of the hot springs and geysers of the Yellowstone National Park, for example, are associated in some way with the presence of Cyanophyceae. Many of the group are also endophytic in habit; that is, they live within cavities of other plants, as in *Anthoceros*, *Azolla*, roots of cycads, etc.; and still others enter into the structure of those composite organisms known as lichens.

A general conception of the group may be obtained by examining a few common forms.

Gloeocapsa.[2]—The adult individual is a single spherical cell (fig. 4), and therefore the body is as simple as it can be, if cells are to be regarded as the units of the gross structure of plants. This single cell consists of a protoplast invested by a wall, and among Cyanophyceae in general the protoplast has no such obvious organization as among the true algae. In general it may be differentiated into two regions: a peripheral zone, colored throughout by the green and blue pigments; and a central region (central body), containing no pigment, and now concluded to be a nucleus. In both regions small granules appear. This differentiation of a pigment region from the rest of the protoplast is not apparent among all the blue-green algae, for in some (as *Gloeocapsa*) the pigments seem to be diffused throughout the protoplast, but in others (as *Oscillatoria*, fig. 6) it is quite

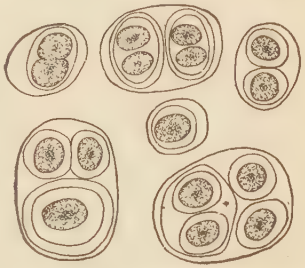


FIG. 4.—*Glocothece:* a single plant in the center, showing the protoplast surrounded by the swollen wall and a layer of mucilage; the other figures show various stages of cell-multiplication, the cells being embedded in the gelatinous matrix produced by their walls.

[1] The precise nature and relations of the pigment or pigments of this group are uncertain. It is possible that there is a single pigment which splits into blue and green constituents.

[2] *Glocothece* is a form closely related to *Gloeocapsa*, from which it differs chiefly in its somewhat elongated cells.

evident, and represents all the organization that has been found in this group. This apparently simple structure of the protoplast is in striking contrast with that found in the true algae and in all higher plants.

The division of the cell is of equal simplicity, for it takes place by the development of a ringlike wall which grows inward and cuts the protoplast in two, the central body (or nucleus) also playing a part. This process of cell-division is the only method of reproduction among the Cyanophyceae, a method known as vegetative multiplication, and meaning that an ordinary working cell (individual) divides and forms two new individuals.

In *Gloeocapsa* the cells may be observed in various stages of division, but the multiplying cells (individuals) are held together mechanically in a gradually accumulating gelatinous matrix (fig. 4), this swelling mucilaginous material being derived from the cell walls, which are being renewed constantly from within by the protoplast. This formation of mucilage by the walls and the imbedding of cells is characteristic of the Cyanophyceae. These groups of cells held together mechanically are spoken of as colonies. In *Gloeocapsa* the colonies are irregular and indefinite, but among other Cyanophyceae they will be observed to assume very definite forms.

FIG. 5. — *Merismopedia:* a portion of a colony, showing the one-celled plants in rectangular arrangement, and all held together by the gelatinous matrix; in one case cell-division has not been completed.

Merismopedia. — In this form, very common in ponds, the cells are arranged so as to produce a remarkably regular rectangular colony (fig. 5). It is evident that this rectangular form is determined by a series of perfectly regular and simultaneous divisions in two directions.

Oscillatoria. — In this well-known form the colony has become a simple filament, and the mucilage sheath is so thin as to be visible only in specially prepared sections (fig. 6). In the related *Lyngbya* the sheath is quite evident. In these forms a filament is built up because the successive cell-divisions are all in the same direction. Each cell of the *Oscillatoria* filament, excepting the end ones, has the form of a short cylinder, indicating that the ends of each cell have been flattened by the pressure of the contiguous cells. At the end of the filament the free surface of the end cell is seen to be convex; and where some cell in the filament has become destroyed, as mentioned below, the adjacent

walls of the two neighboring cells are observed to bulge out. The filament does not grow indefinitely in length, but breaks up now and then by the disorganization of one or more cells, and each fragment begins to construct another colony. This process of fragmentation results in the multiplication of colonies, which may be called colonization.

The protoplast of *Oscillatoria* exhibits the two regions described under *Gloeocapsa* for Cyanophyceae in general; in fact, this differentiation is probably more evident in *Oscillatoria* than in any other common form. The most striking feature of the plant, however, is the characteristic swaying and revolving movement of the filaments, a movement which suggested the name. If a mass of filaments be placed on a solid substratum, the filaments begin a creeping movement and become spread out radiately in a film. It is evident that this movement is possible only as the cells of a filament work together, and this introduces into a colony of cells the idea of an individual composed of many cells. In fact, the many-celled colony merges so gradually into the many-celled individual that there is no boundary between the two.

FIG. 6. — *Oscillatoria:* the cells of the simple filaments show the differentiation of the protoplast into the peripheral pigment region and the central region; in the center of the latter there appears an irregular aggregation of dark material (*chromatin*) characteristic of a nucleus.

Nostoc. — In this form the colony is also a filament, but when the cells divide, they so nearly separate and round off that they become tangent to one another, resulting in a filament resembling a string of beads. Each filament has its own mucilaginous sheath, as in *Lyngbya*, but there is an extraordinary development of mucilage in connection with groups of filaments. As a consequence, *Nostoc* appears in nature as lumps of jelly, in which numerous filaments are found embedded (figs. 7, 8).

The most noticeable fact in reference to these filaments is that the cells are not all alike. At intervals cells appear which differ in contents and usually in size from the ordinary working cells. They are derived from ordinary working cells, which usually enlarge, lose their contents, and become thick-walled. The loss of pigments makes these cells stand out very distinctly in the filament. They are called *heterocysts*, but

this means only "other cells," and suggests nothing as to their behavior. By means of the heterocysts, therefore, the working cells of a filament

FIGS. 7, 8.—*Nostoc:* 7, the jelly-like mass in which the filaments are embedded; 8, filamentous colonies coiled within the gelatinous matrix; four heterocysts shown, dividing the filaments into hormogonia.

are separated into distinct sections, and these sections are called *hormogonia*. It has been observed that when colonization occurs, the heterocysts anchor the filament, and that the hormogonia break loose from them and wriggle out through the jelly-like matrix and establish new colonies. So far as observed, therefore, this differentiation of heterocysts seems to be associated with the fragmentation of the filament.

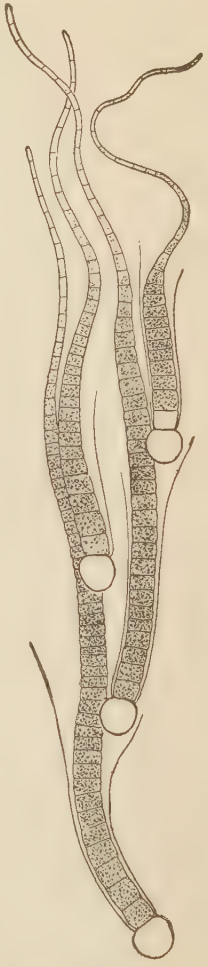


FIG. 9.—*Rivularia:* the filaments show the basal heterocysts and the whip-like extension of the apex.

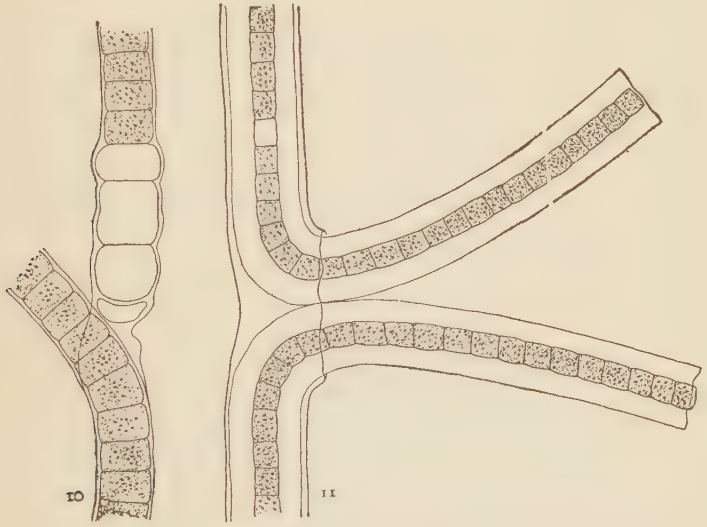
Nostoc illustrates well an ordinary plant method of enduring an unfavorable season, as winter. At the inception of the period of danger, certain cells of the filament enlarge, accumulate reserve food, and become thick-walled. These cells are able to endure cold or drought; and upon the return of favorable conditions, the heavy wall is broken through and a beginning filament emerges. These resting vegetative cells are

often called *arthrospores*, but they are not spores in the same sense as are those which characterize higher plants. In its life history, therefore, *Nostoc* displays three kinds of cells: vegetative cells, heterocysts, and resting cells.

A common form very closely related to *Nostoc* is *Anabaena*, whose name ought to be familiar, but whose separation from *Nostoc* need not be attempted by the elementary student.

Rivularia. — This form may be taken to represent the extreme differentiation of a colony. It is a compact, filamentous plant, like *Oscillatoria;* but the basal cell of the filament is a heterocyst, and the apex of the filament tapers into a very slender, whiplike extension (fig. 9). In this case the filament has a distinct base and apex.

Tolypothrix. — This plant serves to illustrate what is called false branching. It is a filament with distributed heterocysts, and, therefore, composed of several



FIGS. 10, 11. — False branching: 10, *Tolypothrix*, showing false branching by a hormogonium pushing past a heterocyst; 11, *Scytonema*, showing false branching by the pushing outward of two abutting cells of a hormogonium, each of which continues division.

hormogonia. In some cases the end of a hormogonium pushes past a heterocyst and continues division, giving the appearance of a lateral branch (fig. 10). In other cases, as in *Scytonema*, a hormogonium may continue to increase in length without breaking away from the heterocysts, and the pressure results in pushing some two abutting cells outward, each of these two cells then being free to continue the development of a filament (fig. 11).

Stigonema. — In some Cyanophyceae, however, true branching occurs, and this is illustrated by such forms as *Stigonema*, in which branches are started by lateral outgrowths from individual cells of the filament rather than by mechanically freeing some of the cells (fig. 12).

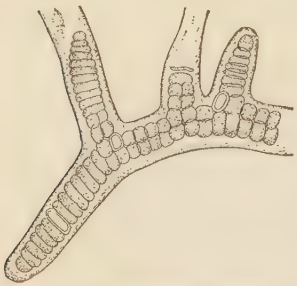


FIG. 12. — *Stigonema:* showing true branching. — After BORZI.

Conclusions. — A brief summary of the important features of the Cyanophyceae may be stated as follows: —

(1) The plant body is a single cell, and the general tendency is to organize a colony of cells into the form of a simple filament.

(2) There is a characteristic mucilaginous swelling of the walls, which favors colony formation by imbedding the individual cells.

(3) The protoplast is apparently simple in organization, giving no evidence of distinct chloroplasts, and with a nucleus ordinarily not sharply limited by a membrane, both of which features are in contrast with the protoplasts of true algae.

(4) There is some differentiation of cells, notably in the formation of heterocysts; and differentiation reaches its extreme expression in such forms as *Rivularia*, with base and apex.

(5) The power of locomotion is evident in the group, notably in *Oscillatoria*, and also in connection with colonization by means of hormogonia.

(6) The only method of reproduction known is vegetative multiplication, and the cell divides by an ingrowing wall plate.

(7) Protection against unfavorable conditions is provided for by the transformation of ordinary vegetative cells into resting cells, the chief changes being enlargement, accumulation of reserve food, and a heavy wall.

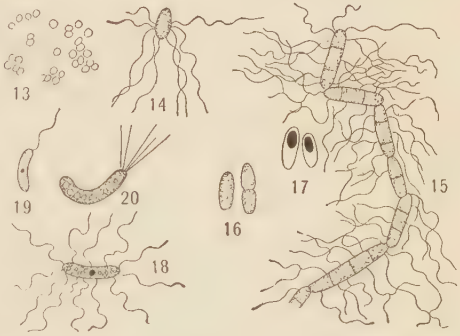
(2) SCHIZOMYCETES

General description. — The name means fission fungi, and corresponds in form to Schizophyceae (fission algae), a name often applied to the blue-green algae. However, they are best known as *bacteria*. The group has many characters in common with the Cyanophyceae, such as the one-celled body which often forms filaments (colonies), a protoplast of simple structure, the tendency in certain conditions to produce a mucilaginous matrix that embeds the cells, the power of locomotion, and

reproduction only by vegetative multiplication, the cell-divisions being simple but in remarkably rapid succession. However, in most forms there is no chlorophyll, so that bacteria in the main are parasites and saprophytes.

The immense economic importance of bacteria has stimulated their investigation to such an extent that bacteriology has become a distinct field of research, with its special technique. An outline of plant morphology can only indicate the existence of this great region of research, for to enter it would demand a course in bacteriology; but bacteria are plants, and their general place among other plants must be considered.

Bacteria include the smallest known organisms, cells having been measured that are only 0.0005 mm. in diameter. The cells are either solitary or they may form filaments, as among the Cyanophyceae. For general purposes, individual cells are often referred to three form groups: *coccus* forms, in which the cells are spherical; *bacterium* or *bacillus* forms, in which the cells are oblong or have the form of short rods; and *spirillum* forms, in which the cells are curved (figs. 13–20). When these various forms of cells enter into the structure of filaments, corresponding variations in the form of the filaments follow.



FIGS. 13–20. — *Bacteria:* 13, coccus form, from pus; 14–18, bacillus forms (14–17, hay bacillus); 14, motile cell; 15, filament of motile cells; 16, non-motile cells; 17, cells with "spores"; 18, typhoid-fever form (*Bacillus typhi*); 19, 20, spirillum forms; 19, cholera form (*Vibrio cholerae*); 20, *Spirillum undula*. — After A. FISCHER.

The occurrence of bacteria may be described as almost literally everywhere: in waters of every depth, in air, in soil, in all organic bodies, living or dead, etc. Their resistance to conditions impossible for other plants to endure is remarkable — a feature suggested by their associates, the Cyanophyceae. Extreme cold, high temperatures, and desiccation that would destroy ordinary plants are successfully withstood by bacteria.

Structure. — The structure of the bacterial cell appears to be extremely simple; in fact it may be said to be almost structureless. The proto

plast is invested by a membrane, appears to be homogeneous, and usually contains a few granules. It seems not to have even such simple differentiation as occurs in the cells of certain Cyanophyceae; but in all such cases it must be kept in mind that we are dealing with very minute objects and that presently a technique may be developed that will reveal an amount of organization that we have no means of seeing at present.

Many of the bacteria are ciliated, the cilia being distributed over the body in various ways, and always extremely difficult to detect. These ciliated forms are very active, and their movements have suggested that bacteria are animals. Under certain conditions many bacteria pass into a quiescent stage and collect in colonies that are held together by a gelatinous matrix formed from the walls. These quiescent colonies, thus embedded, form characteristic pellicles on nutrient media, as on a decoction of hay, on bouillon, on stagnant water, and on various solid media. This quiescent, pellicle-forming stage is known as the *zoogloea* stage.

Multiplication. — The multiplication of cells by division is exceedingly rapid, the progeny of one cell in twenty-four hours often running into many millions. As already said, these newly formed cells either separate or hang together in filaments. When the nutritive supply fails, the protoplasm condenses in the middle or end of the cell and becomes invested by a heavy membrane. These are the so-called spores, but they are really resting cells such as are formed among the Cyanophyceae, except that they are formed within the old cell. These resting cells are even more resistant than the ordinary vegetative cells. In favorable conditions the protecting membrane bursts and the protoplast resumes active division.

Cultures. — It is very difficult and often impossible to recognize species of bacteria by the appearance of the individual cells, but in mass cultures the colonies are often very distinct in form, color, structure, and effect on nutrient media. These mass cultures are made in liquid media or upon solid media (gelatin, agar, potato, etc.). For purposes of investigation pure cultures are absolutely necessary, which means the separation of the form under investigation from every other form with which it may be associated, a process requiring a special technique.

Activities. —Many bacteria are peculiar in that they are able to live in the absence of free oxygen, which in other plants is associated with the fundamental process of respiration. Such bacteria are called

anaerobic, the contrasting term for those bacteria that need free oxygen being *aerobic*. These are not names of groups, but of two modes of life that may be found in any group. The activities and effects of bacteria are remarkable, many of them holding a most important relation to human interests. A very brief statement of some of these activities must suffice, but it may serve to indicate the economic importance of the group.

Saprophytic bacteria. — These forms attack the dead bodies or the organic products of plants and animals, and bring about putrefaction and fermentation. When they are excluded from such organic material, it does not decay or ferment, and the process of canning, for example, is intended to effect this exclusion. When protein material is attacked and broken up, there is an escape of ill-smelling compounds, causing the offensive odor associated with putrefaction. In fermentation, complex carbohydrates are attacked, and simpler substances, such as alcohol, carbon dioxid, lactic acid, butyric acid, etc., are produced from them, according to the kind of bacteria at work.

Pathogenic bacteria. — These are the disease-producing forms, their activities being connected with living organisms. The disease is the result either of a direct attack upon the tissues, or of the excretion of a poison (toxin), or of both. Modern medicine and surgery are largely based upon excluding or destroying or neutralizing these forms. Such diseases as erysipelas, tetanus, diphtheria, tuberculosis, typhoid fever, pneumonia, cholera, pear blight, cabbage rot, etc., are known to be bacterial diseases. Besides the dangerous forms which occasionally attack human beings, there are numerous harmless forms constantly present throughout the alimentary tract.

Nitrogen bacteria. — These are certain bacteria of the soil that are able to utilize the free nitrogen that exists in such abundance in the air. Ordinary green plants can use nitrogen only in certain of its compounds, so that the power of these bacteria is both remarkable and important. They are best known in connection with the tubercles of certain Leguminosae (figs. 1101, 1102), as the clovers, which can be used, therefore, in the restoration of nitrogen compounds to impoverished soil (see p. 379).

Nitrifying bacteria. — These are also soil forms, and although they contain no chlorophyll, they can manufacture their own food. They can obtain carbon from carbon dioxid, without the presence of either chlorophyll or light; and their "nitrification" consists in taking ammonia (and other simple nitrogen compounds) and oxidizing it to nitrous

acid so that nitrites are formed, when these in turn are oxidized to nitrates, which are nitrogen-containing compounds available for green plants.

Iron bacteria. — These forms live in iron-containing waters, and as a result of their activities iron oxid is deposited in the gelatinous matrix. This characteristic reddish slimy deposit is exceedingly common about iron springs and their outlets.

Sulphur bacteria. — These bacteria are able to oxidize sulphuretted hydrogen, storing free sulphur in their cells. Most conspicuous among them is a high-grade filamentous form (*Beggiatoa*) closely resembling the filamentous Cyanophyceae.

These statements illustrate the remarkable powers found among bacteria, and when they are grouped together, the list is a striking one. A group which is remarkably resistant to external conditions that destroy other plants, which can manufacture carbohydrate food without chlorophyll or light, which can use free nitrogen, which can live without oxygen, is suggestive of the possibilities of plant life under conditions that would forbid all existing vegetation.

Myxobacteriaceae. — This group of organisms has been recognized recently, and is evidently related to the bacteria, as the name suggests; but it is distinguished from them by a remarkably complex colony organization. The individual cells resemble those of the bacteria, but they are combined in structures of definite and often elaborate form. For example, one colony resembles a stalk bearing a group of sporangia at its summit. The life histories of the individual cells are like those of the bacteria, and resting cells (so-called spores) are formed in the same way, from which rodlike cells escape and assemble to organize the complex colony. The name suggests a combination of the characters of slime molds and bacteria, the individual cells resembling the latter, and the cells coming together to form a complex body, as the plasmodium of the slime molds is formed. The group is included here because of its resemblance to the bacteria, but it must not be inferred that it belongs to the schizomycetes or even to the schizophytes. It must remain at present as one of the thallophyte groups of uncertain position.

3. ALGAE

These make up the great chlorophyll-bearing assemblage of thallophytes, capable of manufacturing food (see p. 363), and representing the forms from which the higher groups of plants have probably been derived. The three groups of algae are named from their characteristic pigments, as follows: *Chlorophyceae* (green algae), *Phaeophyceae* (brown algae), and *Rhodophyceae* (red algae). These differences in pigments are associated with important differences in structure, which will appear as the forms are discussed.

(1) Chlorophyceae

General character. — The green algae usually contain no pigment in addition to the chlorophyll, and their appearance justifies the name. They include the simplest algae, and are generally supposed to be the forms from which the higher groups of plants have been derived. On this account green algae may be regarded as the beginning of our present vegetation. The protoplast always has a distinct nucleus and one or more chloroplasts, and this mode of organization is continued throughout all the higher green plants. As presented here, the Chlorophyceae contain six distinct groups, as follows: *Volvocales*, *Protococcales*, *Confervales*, *Siphonales*, *Conjugales*, and *Charales*. It is recognized that some of these groups are very artificial, and that some of them perhaps should be set apart from the Chlorophyceae; but in this elementary presentation of the forms, it is more convenient and less confusing to use this grouping. The doubtful situations will be indicated in connection with the different groups.

(a) Volvocales

General character. — These aquatic forms are distinguished from other green algae by the fact that the vegetative cells have cilia and therefore are motile. They are sometimes regarded as animals, for they grade plainly into the Flagellates, a group of organisms of mixed plant and animal affinities (see p. 20). A few representative forms will indicate the structure and tendencies of the group.

Chlamydomonas and Sphaerella. — *Chlamydomonas* consists of a single cell bearing two cilia, the protoplast being closely invested by a thin membrane (fig. 21). The structure of *Sphaerella* is in general the same except that the cell has a loose membrane, which is connected with the protoplast by strands and is pierced by the two cilia (fig. 22).

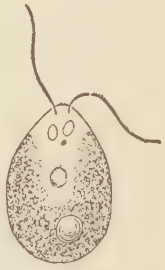


Fig. 21. — *Chlamydomonas:* showing the large cuplike chloroplast, the embedded pyrenoid, the centrally placed nucleus, the two contractile vacuoles, the red pigment spot, and the two cilia. — After West.

Fig. 22. — *Sphaerella:* showing the protoplast invested by a loose membrane, which is pierced by the two cilia. — After West.

Structure. — The structure of the protoplast of *Chlamydomonas* (fig. 21) may be taken as representative of the whole group. There is usually a single, large, cup-shaped chloroplast at the larger end of the protoplast, in which is embedded a large protein body (*pyrenoid*). In the cup of the chloroplast the nucleus is found; near the base of the cilia are two contractile vacuoles; at the forward end a red pigment spot ("eye spot") is observed; and two long apical cilia complete the equipment. The cells are very active and their motion is influenced by light, to which the "eye spot" is supposed (without adequate ground) to be very sensitive. In some forms a red pigment appears so abundantly as to give a reddish hue, giving rise to the accounts of "red pools" and "red snow." Under certain conditions the cell may drop its cilia and become quiescent, and this temporary loss of motility in the vegetative cells of Volvocales becomes the permanent condition in higher forms.

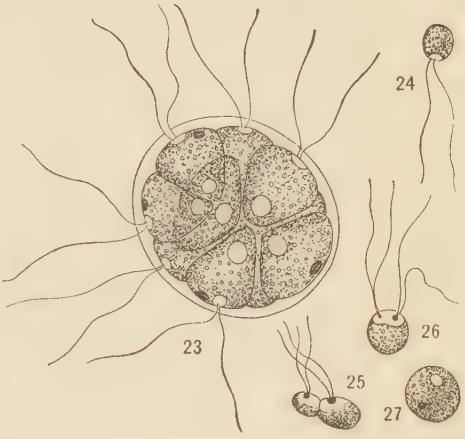
Reproduction. — In this quiescent stage, the protoplast may divide into several new cells, which escape as new and active individuals. These daughter cells, formed within the old mother cell, are called *zoospores* (swimming spores, swarm spores), but they are also the adult form of the plant. Therefore, the ordinary vegetative cells of Volvocales are like the zoospores of the higher forms, in which the vegetative cells and zoospores are quite distinct.

Certain cells form more numerous and smaller zoospore-like cells, which escape, swim freely, and fuse in pairs to form new cells (figs. 24–27). This is a sexual process, and therefore these pairing cells are called *gametes* (sexual cells). Since the pairing gametes are alike, the condition is called *isogamy*, and the plants are said to be *isogamous*. It is evident that the gametes are related to the zoospores, and it is thought that they are only modified zoospores. The origin of gametes is the origin of sex, and isogamy is the simplest form of sexuality. This fusion of two gametes to form a single cell is the act of fertilization, but to distinguish it from the higher forms of fertilization it has become customary to call the fusion of similar gametes *conjugation*. The cell resulting from conjugation is a *zygospore* (or *zygote*), spore being the general name of a cell set apart for reproduction, and the prefix in this case indicating that the spore has been formed by conjugation. In isogamous plants, therefore, the gametes conjugate and produce a zygospore. In general the zygospore is a resting cell, being formed at the inception of unfavorable conditions, having a heavy wall, and starting new generations upon the return of favorable conditions. In

the case of *Sphaerella*, when the zygospore germinates, the protoplast divides, forming two or four cells, which escape as free-swimming cells.

It should be remarked that reproduction by zoospores (an asexual method) results in multiplying plants during the growing season; while reproduction by zygospores (the sexual method) is connected with the formation of a protected cell which endures unfavorable conditions.

Pandorina. — Among Volvocales, as among the previously described groups, there is a prevailing tendency to colony formation, which finally reaches an extreme expression. *Pandorina* illustrates a simple colony, which is composed usually of sixteen similar cells held together by a gelatinous matrix (fig. 23). The protoplast of any cell of the colony may divide into sixteen daughter cells, which form a new colony that escapes from the mother cell and from the mother colony. There is also sexual reproduction as described above, the gametes being produced just as are the daughter colonies. The pairing gametes are similar, and therefore *Pandorina* is isogamous and the sexually formed spore is a zygospore (figs. 24–27).



FIGS. 23–27. — *Pandorina:* 23, the free-swimming colony; 24, a gamete; 25, two gametes beginning to fuse; 26, fusion of gametes almost complete; 27, the zygospore. — After PRINGSHEIM.

Eudorina. — In this form there is a larger colony or cell family. New families are formed as described for *Pandorina*, but sexual reproduction is different (fig. 28). Certain cells of the colony, not much different from the vegetative cells, assume the function of *eggs*. Other cells divide to form groups of *sperms*, which hang together in a plate, but finally break up and fuse with the eggs. In this case the pairing gametes (egg and sperm) have become very dissimilar, and hence the condition is called *heterogamy*, the plant being *heterogamous*. The larger gamete, often called the *oosphere*, is better called the egg; and the smaller one, often called *antherozoid* or *spermatozoid*, is better called the sperm. The

process of fusion in this case is called *fertilization*, and the product is an *oospore* (fertilized egg).

It is evident that in passing from isogamy to heterogamy there is a differentiation of sex, so that we recognize a male gamete and a female

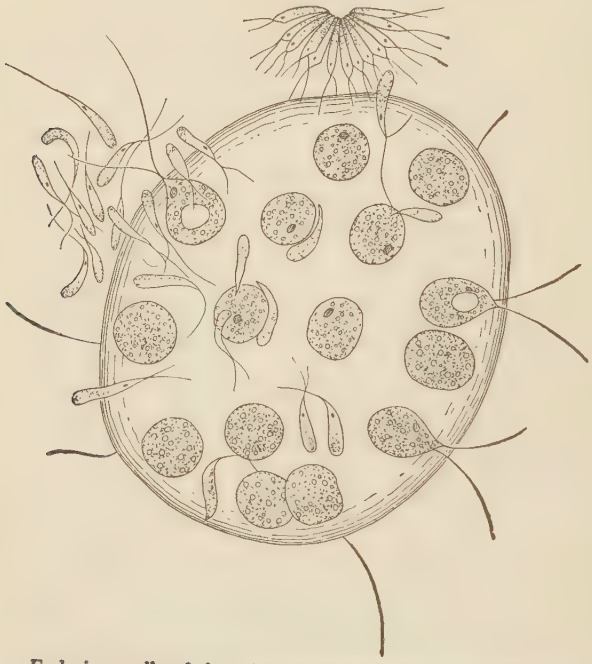


FIG. 28. — *Eudorina:* cells of the colony functioning as eggs, with which sperms are coming into contact; above the colony a group of sperms still hanging together may be seen. — After GOEBEL.

gamete. The female gamete has developed its nutritive supply, and hence its size, at the expense of activity, and finally becomes an entirely passive cell; while the male gamete retains its activity.

Volvox. — In this form the highest expression of colony formation is reached, the free-swimming colony being a hollow sphere composed often of thousands of ciliated cells (figs. 29, 30). These cells are connected by strands of cytoplasm, and therefore the structure may be regarded as a multicellular individual rather than as a colony. At first all cells of the colony are alike, but two kinds of cells may be observed in a mature colony: small vegetative cells which do not divide, and among the thousands of these smaller cells a few (rarely over ten or

twelve) much larger ones which divide to form new colonies. These large colony-forming cells are derived from the smaller cells and have been called *gonidia*, a very inappropriate name.

The sexual reproduction is much as in *Eudorina*, but the eggs become much larger than the ordinary cells and lose their cilia. The sperms, produced by the division of certain cells, are elongated, yellow, and biciliate. Fertilization occurs in the cavity of the colony (fig. 31), and the resulting oospore is a resting, protected cell (fig. 32). Upon germination, there comes from the oospore a group of ciliated cells (equivalents of zoospores) that represent a new colony.

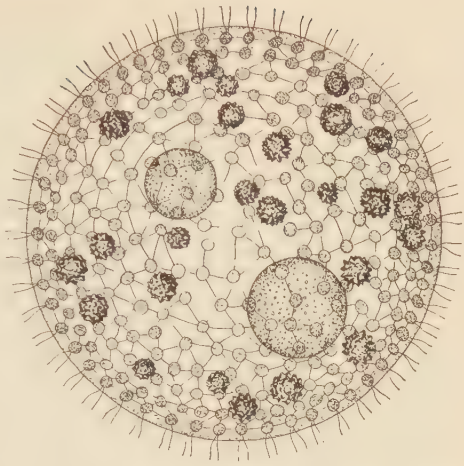
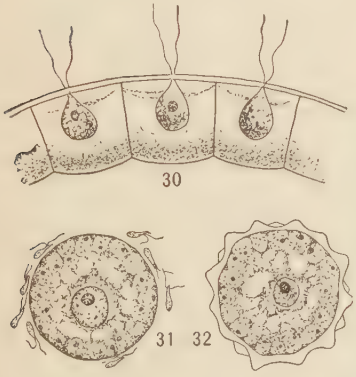


FIG. 29. — *Volvox*: the large globular colony composed of small vegetative cells connected by strands of cytoplasm, two large colony-forming cells, and numerous oospores with rough walls.

In this so-called *Volvox* colony differentiation has resulted in four distinct kinds of cells: ciliated vegetative cells, colony-forming cells, eggs, and sperms.



FIGS. 30–32. — *Volvox*: 30, peripheral cells of the colony (after WEST); 31, an egg surrounded by sperms; 32, an oospore with heavy wall.

Conclusions. — A summary of the features of the Volvocales may be stated as follows: The forms range from isolated cells to complex spherical colonies, all the ordinary cells being ciliate; a new colony is formed from the division of a single mother cell; sexual reproduction is present, advancing from isogamy to heterogamy, that is, from the origin of sex to the differentiation of sex. *Volvox* and its colony-forming allies are to be regarded as specialized forms, and

FIG. 33. — *Euglena:* showing a single cilium (flagellum), a large nucleus, and numerous chloroplasts.

the connection with the next group of green algae is to be sought in such forms as *Chlamydomonas* and *Sphaerella*.

Flagellates. — This problematical group of organisms is so suggestive of a relationship to Volvocales that it should be mentioned in this connection. They are one-celled, active, aquatic forms, with one or two (sometimes more) cilia (fig. 33). The cell is naked or with a distinct membrane, which rarely contains any cellulose. The protoplast shows contractile and amoeboid movements, and contains a nucleus, a pulsating vacuole, and in many forms distinct green or brown chromoplasts. Some of them are very animal-like in taking food, ingesting solid particles; and their usual multiplication by longitudinal splitting is not plantlike. No sexual reproduction is known, but the frequent formation of thick-walled "resting spores" is suggestive of plants. This combination of plant and animal characters has suggested that the flagellates may be regarded as the starting point for such one-celled thallophytes as the Volvocales on the one hand, and for Protozoa on the other. In fact, by some authors Volvocales are included among the flagellates.

(b) Protococcales

General character. — The group of forms included here under this name is probably a very heterogeneous assemblage, and it has been much broken up recently by the special students of algae, but it will serve our purpose. The plants occur mainly in fresh water, ranging from an extreme aquatic habit to occurrence in moist places, such as tree trunks, shaded earth, etc. Some are endophytic, living in the intercellular spaces of certain aquatic seed plants; others enter into the structure of lichens; while still others give the green color to certain animals, as fresh-water sponges, hydra, etc. The possible connection of the solitary (one-celled) forms with such solitary Volvocales as *Chlamydomonas* is apparent, the former being characterized by the absence of cilia on the vegetative cells; in other words, there is an occasional loss of motility by the vegetative cells of Volvocales, and this is the permanent condition of the vegetative cells of Protococcales.

Pleurococcus. — This is an exceedingly common green slime found on flower pots, damp bricks, tree trunks, etc., and it may be regarded as a representative one-celled green plant. If there is any connection between Protococcales and Volvocales, it is through such forms as

Pleurococcus (fig. 34). The globular cell has a definite wall, a central nucleus, and a large lobed chloroplast whose lobes suggest several chloroplasts. These cells multiply rapidly by division, and they may be seen clinging together in irregular groups. No other method of reproduction is known, so that the life history is exceedingly simple.

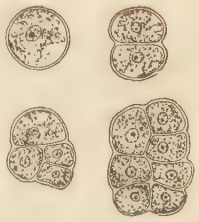
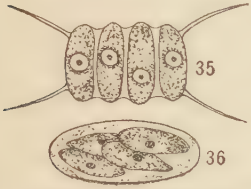


FIG. 34. — *Pleurococcus:* the single cell with its nucleus and large chloroplast, and cell-groups of various sizes.

The other forms selected as illustrations are colony formers, this tendency being as striking as among the Volvocales.



FIGS. 35, 36. — *Scenedesmus:* 35, colony of four cells; 36, cell forming a new colony.

Scenedesmus. — This form represents the simplest colony, consisting of two to eight cells lying side by side, the end cells often with more or less conspicuous appendages (fig. 35). Each cell divides internally to form a new colony (fig. 36), and no other method of reproduction is known.

Pediastrum. — The colony in this form is a floating or suspended, more or less star-shaped plate of polygonal cells, sometimes as many as sixty-four in number (fig. 37). Within any cell distinct zoospores are formed, which escape from the mother cell inclosed by a delicate membrane and then become arranged into a new colony (figs. 37–39). Sexual reproduction is also present in its simplest form, certain cells forming zoospore-like cells, smaller and more numerous than the zoospores, which function as gametes (figs. 40–44). *Pediastrum*, therefore, is isogamous, forming zygospores that are resting or protected cells.

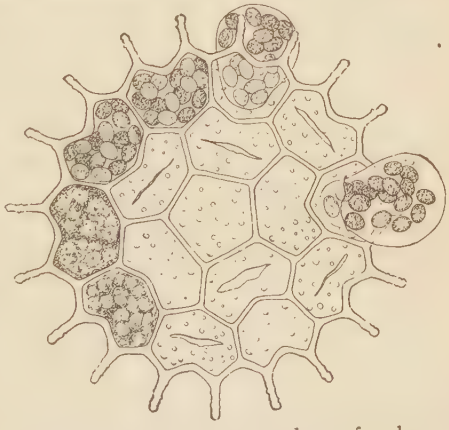
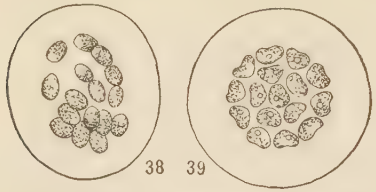


FIG. 37. — *Pediastrum:* a colony of polygonal cells, some of which are forming new colonies; two colonies escaping from the mother colony.

Hydrodictyon. — This is the well-known water net,

one of the most remarkable of plant colonies. This hollow net is freely floating, and sometimes attains a length of 25 to 30 cm. It is formed by an end-to-end union of long cylindrical cells in such a way as to form polygonal meshes, three or four cells abutting at each junction (fig. 45). The cytoplasm forms a thick layer inclosing a large central vacuole, and the chloroplast is an irregular plate that finally breaks up into many small chloroplasts.



FIGS. 38, 39. — *Pediastrum:* cells with daughter colonies in different stages of formation. — After A. BRAUN.

When the cell reaches a certain size, the protoplast divides into very numerous (7000 to 20,000) biciliate zoospores, each with a nucleus and a small chloroplast (fig. 46). These zoospores do not escape, but swim about freely for a time within the large mother cell, come to rest, and gradually develop a small net within the mother cell (fig. 47). The wall of the mother cell finally softens and the young net is set free and grows to adult size without any cell division.

FIGS. 40–44. — *Pediastrum:* 40, zoospore; 41, gamete; 42, 43, gametes fusing; 44, zygospore. — After WEST.

The sexual reproduction is isogamous, certain cells producing a remarkable number of gametes (30,000 to 100,000), which escape from the mother cell at once and fuse in pairs, forming zygospores (figs. 48–50). Experiments upon *Hydrodictyon* have succeeded in securing at will the production of zoospores (forming young nets)

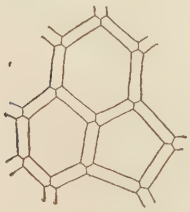


FIG. 45. — *Hydrodictyon:* arrangement of cells in forming the net. — After WEST.

FIG. 46. — *Hydrodictyon:* zoospores within a mother cell beginning to form a net. — After KLEBS.

or of gametes, by using various nutrient media. The zygospore is a heavy-walled resting cell that settles to the bottom of the water and resembles a *Pleurococcus* cell. After a more or less prolonged resting period, the zygospore produces two or four large biciliate zoospores, which escape into the water (figs. 51, 52) and develop into large, irregular, many-angled, thick-walled cells (polyhedra), which persist through the winter (fig. 53). Upon the return of favorable conditions, each of these polyhedra (resting cells) forms internally a small net of 200 to 300 cells (fig. 54), which escapes, and the multiplication of nets is begun. It is a noteworthy fact that

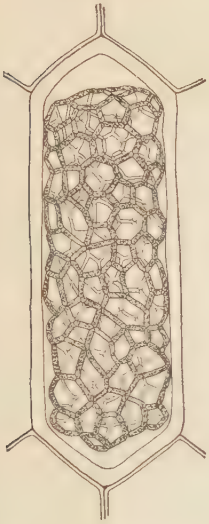
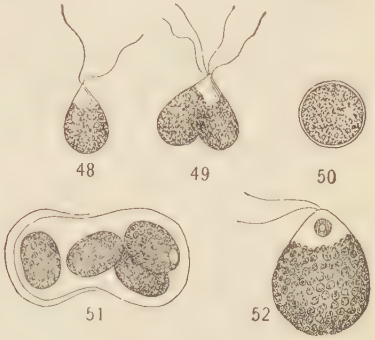
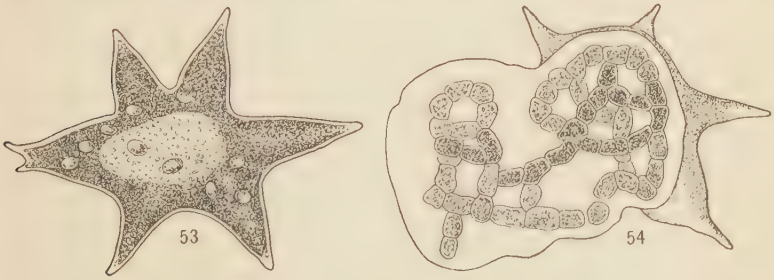


FIG. 47. — *Hydrodictyon:* a completed young net within its mother cell. — After KLEBS.



FIGS. 48–52. — *Hydrodictyon:* 48, gamete; 49, gametes fusing; 50, zygospore; 51, four zoospores developed by the zygospore; 52, zoospore escaped from zygospore. — 48–50, after KLEBS; 51, 52, after PRINGSHEIM.



FIGS. 53, 54. — *Hydrodictyon:* 53, polyhedron formed by a zoospore; 54, young net forming within a polyhedron. — After PRINGSHEIM.

the zygospore does not produce a net directly, but gives rise to other cells which do.

Conclusions. — Taking the whole assemblage of forms included here under Protococcales, the range of form is from a solitary cell to a complex colony, *Hydrodictyon* holding the same highly specialized position in this series that *Volvox* does among the Volvocales. A marked feature of difference, however, is that the vegetative cells are not motile. Colony reproduction occurs as among the Volvocales, the zoospores produced by a mother cell being held together or retained until they are organized into a new colony. The lowest forms of Protococcales exhibit no sexual reproduction, but among the higher forms isogamy is attained; while among Volvocales heterogamy is reached.

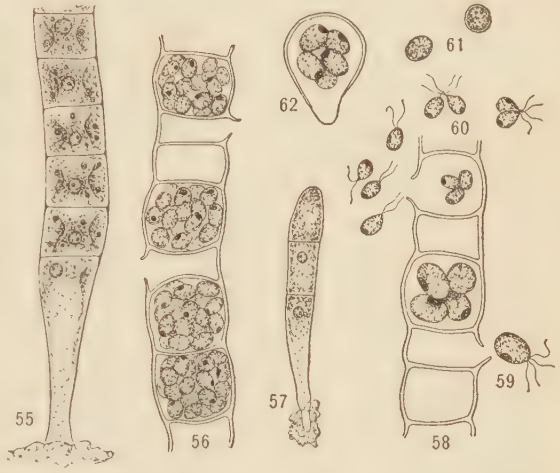
(c) Confervales

General character. — Under this name what may be regarded as the representative green algae are assembled. The assemblage is a very artificial one, and it has been broken up and scattered by the special students of algae, but for our purpose it is convenient to consider these forms together. They are nearly all aquatic, usually filamentous, and always septate (with cross walls). Under certain conditions these filamentous bodies may break up into isolated cells and remain in this condition for a time, resembling the forms of Protococcales with isolated cells, as *Pleurococcus*. All of them produce zoospores, and it is probable that all of them have some form of sexual reproduction. In considering certain representative forms, two categories are convenient; namely, the isogamous forms and the heterogamous forms.

(*a*) *Isogamous forms*

Ulothrix. — This very common alga may be taken to stand for a representative isogamous conferva form. It is a simple filament, whose basal cell is modified to form a holdfast that anchors the body and permits a permanent position in moving water (fig. 55). The ordinary vegetative cells are short, and each one contains a nucleus and a large chloroplast which is peripherally placed and has the form of a thick hollow cylinder. Any of the cells may produce zoospores, which may range in number from one to thirty-two even in the same filament (fig. 56), the size of the zoospore depending upon the number of divisions. A large zoospore bears four cilia (fig. 59), and resembles a vegetative

cell of the Volvocales, even to the "eye spot" and contractile vacuoles. The spores escape through an opening in the wall of the mother cell, swim about, come to rest, settle upon some support, ciliate end foremost, develop a holdfast, begin cell division, and new filaments are started (fig. 57). This differentiation between zoospores and ordinary vegetative cells, and the behavior of the zoospores in escaping individually from the mother cell and starting independent individuals, are features in contrast with the ordinary situation among the Volvocales and Protococcales. In any event, it should be kept in mind that the zoospore type of cell is probably to be regarded as the most primitive type among the green algae.



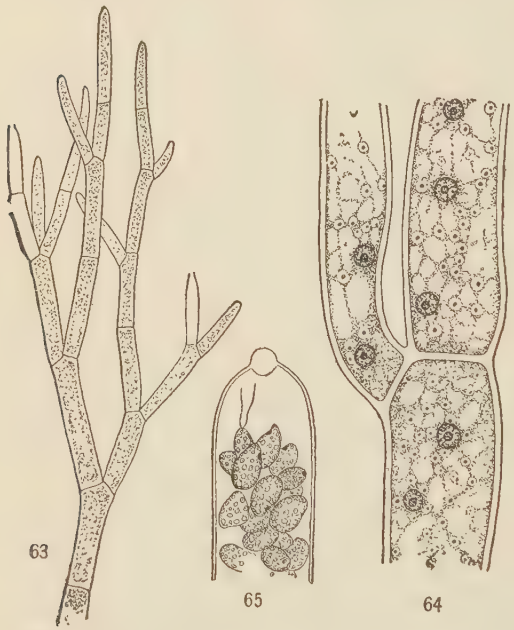
FIGS. 55–62. — *Ulothrix:* 55, base of filament with holdfast; 56, filament producing zoospores or gametes; 57, young filament developed from zoospore; 58, filament discharging zoospores and gametes; 59, an escaped zoospore; 60, escaped and pairing gametes; 61, zygospores; 62, zygospore producing zoospores. — 55–61, after COULTER; 62, after DODEL-PORT.

The sexual reproduction is isogamous, the gametes being produced just as are the zoospores, but differing in usually being smaller, and of course more numerous, and in being biciliate (fig. 60). The freed gametes conjugate in pairs and form zygospores (fig. 61), which after the resting period do not give rise to new filaments directly, but produce several zoospores (fig. 62) that give rise to filaments. This intercalation of zoospores in the life history between the zygospores and the new filaments is an important fact to note.

Ulothrix is very often used to illustrate the origin of sex among the green algae. In many forms the vegetative cells are found producing swimming cells of all sizes, varying from the large zoospores to the small gametes, so that it is often impossible to distinguish between zoospores and gametes by their appearance. Some of the swimming cells

that are smaller than zoospores and larger than gametes, and which have two or four cilia, germinate slowly in producing filaments, but are evidently zoospores in behavior. Under certain conditions, also, some of the smaller swimming cells that ordinarily function as gametes produce small filaments, thus functioning as zoospores. These facts have suggested that gametes are derived from zoospores; that is, that the sexual cells are simply very small zoospores, which fuse in pairs before germination.

Ulva. — This is the well-known sea lettuce, a marine form, with a membranous flat thallus, like a leaf in appearance but not at all in structure. It is interesting in being a flat sheet of cells rather than a filament, but it shows the same reproductive level as *Ulothrix*, the zoospores and gametes being of the same general kind. The zygospore, however, instead of giving rise to zoospores, as in *Ulothrix*, produces a new thallus directly.



FIGS. 63–65. — *Cladophora:* 63, portion of branching filament; 64, enlarged cells, showing several nuclei in each cell and numerous pyrenoids (after CHAMBERLAIN); 65, portion of tip cell forming biciliate zoospores (after STRASBURGER).

Chaetophora. — This form illustrates a freely branching filamentous body, in this case the branches bearing hairlike terminations, a character indicated by the name. The zoospores and gametes are as in *Ulothrix* and *Ulva*.

Stigeoclonium. — The body of this form is of the same general type as that of *Chaetophora*, and with the same methods of reproduction. It displays in a striking way a feature more or less characteristic of all filamentous Confervales, being remarkable for passing long periods as a one-celled plant. Under certain conditions the cells of a filament, when they divide, round off and separate, this one-celled stage being called the *palmella* form.[1] Under different conditions the filamentous form is resumed (figs. 858–860).

[1] The name *Palmella* was given to the one-celled form before its relation to *Stigeoclonium* and other Confervales was known. It is now retained to indicate the one-celled stage.

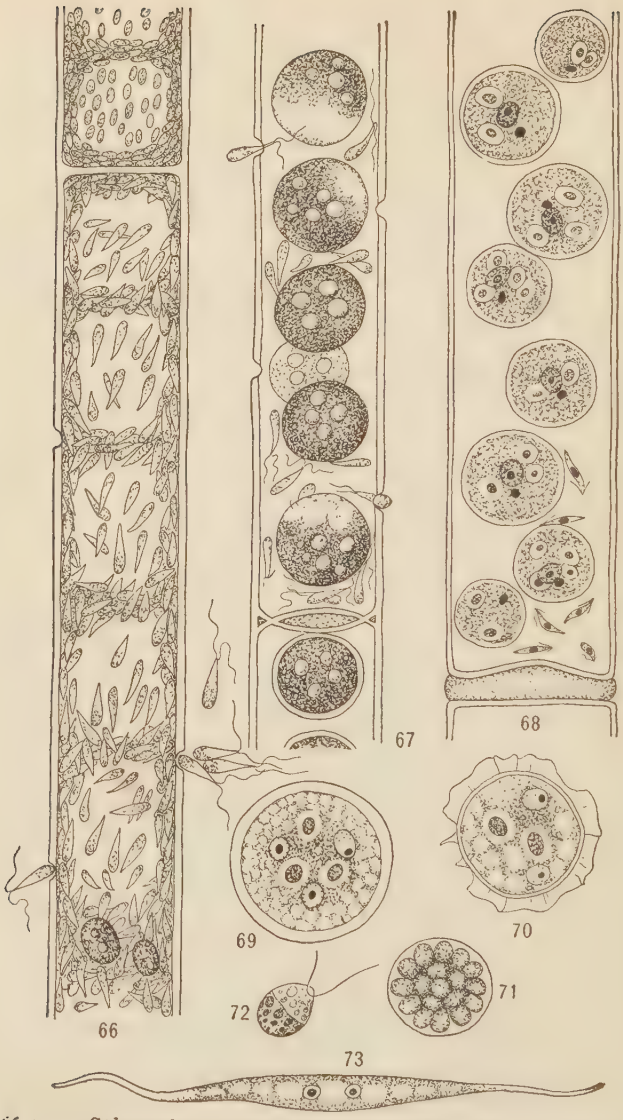
These changes from the filamentous to the palmella form and back again have been brought under experimental control (see Part III).

Cladophora. — This is one of the most common of the green algae, being a profusely branching and anchored filamentous form, the branches arising from the upper ends of the elongated cells (fig. 63). The cells are remarkable in containing many nuclei, such multinucleate cells being called *coenocytes* (fig. 64). A filament composed of a series of coenocytic cells suggests a structure on the way towards a completely coenocytic body, such as characterizes the Siphonales (see p. 33). In addition to the nuclei, the *Cladophora* cell contains many chloroplasts in the peripheral layer of cytoplasm, and numerous pyrenoids in the plastids. The cell division in this case is by means of a plate that begins as a ring at the cell wall and growing centripetally cleaves the protoplast. In enlarged apical cells (usually) a very large number of biciliate zoospores are formed (fig. 65), and biciliate gametes may be formed in any cell. The zygospore in germination develops a new filament directly.

(*b*) *Heterogamous forms*

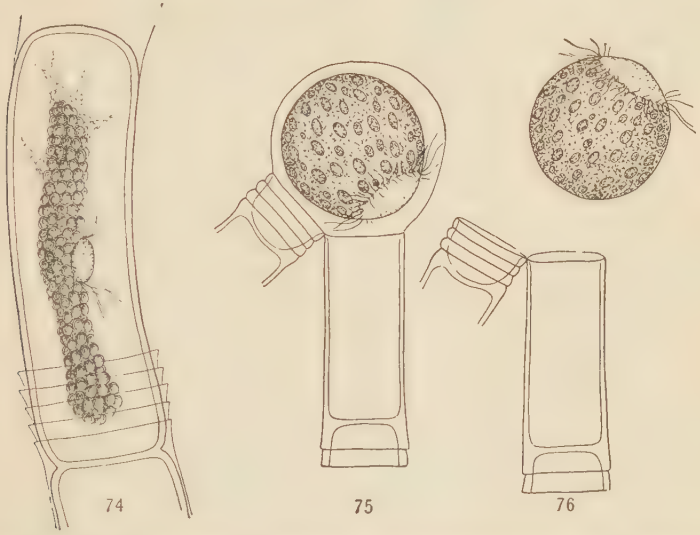
Sphaeroplea. — This form is a simple filament, with multinucleate (coenocytic) cells, as in *Cladophora*, and there is the same abundant development of zoospores. In sexual reproduction, however, two kinds of gametes are produced; one being the usual biciliate, zoospore-like cell (the sperm); the other being a larger cell, with no cilia (the oosphere or egg). The cell producing the numerous sperms is an *antheridium* (fig. 66), and the cell producing the several eggs is an *oogonium* (fig. 67); but in this case antheridia and oogonia are vegetative cells, unchanged in form. In the same way, the cells producing zoospores may be called *sporangia*, but it is not usual to apply these names until these cells become distinct in appearance from the vegetative cells. The sperms find entrance into the oogonium and fertilize the eggs, the resulting oospores being protected cells (figs. 67–70). In germination the oospore produces a number of zoospores (figs. 71, 72), which in turn give rise to new filaments (fig. 73).

Oedogonium. — This very common alga is a simple anchored filament of uninucleate cells containing a single peripheral chloroplast. Certain of the vegetative cells produce zoospores, which are large, usually solitary, and with a crown of cilia (figs. 74–76). Other cells of the filament become enlarged and very conspicuous, forming the oogonia,



FIGS. 66–73. — *Sphaeroplea:* 66, cells producing sperms; 67, cells producing eggs, which are surrounded by sperms; 68, eggs immediately after fertilization, each with one nucleus; 69, fertilized egg (oospore) further advanced, with several nuclei; 70, oospore with heavy wall; 71, zoospores formed by oospore; 72, escaped zoospore; 73, young filament produced by zoospore. — 66, 67, 71, after COHN; 68–70, after KLEBAHN; 72, 73, after HEINRICHER.

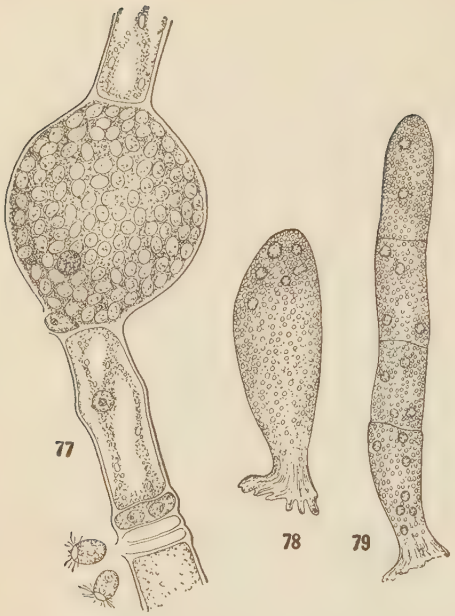
each one of which produces a single very large egg, conspicuously filled with reserve food, and develops a perforation which the sperms enter. Still other cells of the filament divide, the daughter cells not elongating, thus producing a short row of small cells, the antheridia, within each one of which one or two sperms are developed (fig. 77). The sperms are much smaller than the zoospores, but they have the same crown of cilia, and this evident relationship between spore and sperm is constantly



FIGS. 74–76. — *Oedogonium:* 74, large zoospore forming within the cell, including all the contents; 75, zoospore escaping from cell; 76, zoospore freed from its membrane. — 74, after PRINGSHEIM; 75, 76, after HIRN.

appearing. In this case the oogonia and antheridia are distinct from the vegetative cells, but still they are transformed vegetative cells. The sperms escape from the antheridia, swarm about the oogonia, enter them through the perforation, and fertilize the eggs. Although several sperms may enter an oogonium, only one is concerned in the act of fertilization, the essential feature of which seems to be the fusion of the two nuclei. The oospore is a heavy-walled cell, which upon germination produces four zoospores, each one of which gives rise to a new filament (figs. 80–82).

In the form of *Oedogonium* just described, the oogonia and antheridia occur in the same filament, but in certain species they occur on different



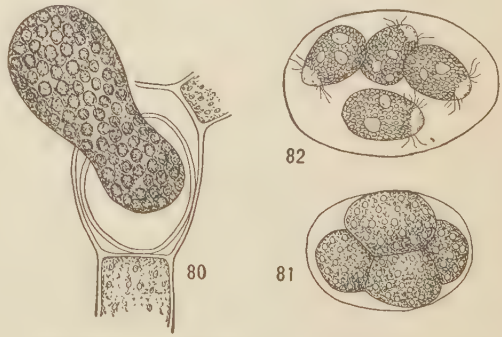
FIGS. 77–79. — *Oedogonium:* 77, portion of a filament showing the large oogonium, which contains an egg filled with food reserve and a single nucleus; at the base of the oogonium a sperm is seen entering; also three antheridia, from two of which sperms have escaped; 78, 79, young filaments developing from a zoospore. — After COULTER.

terminal cells (antheridia) develop sperms that are set free by the opening of the caplike lid (fig. 83).

Bulbochaete. — This well-known form has the same general life history as that described for *Oedogonium*, but it is a branching filamentous form.

Coleochaete. — This is a most interesting and a very much discussed

filaments, which may then be spoken of as male and female filaments. This separation of the sexes in different individuals is a condition called *dioecism*. Among these *dioecious* forms an interesting modification may arise, the male filaments being very much dwarfed. These dwarf filaments are produced by special small zoospores, which are larger than the sperms but smaller than the regular zoospores, and are called *androspores* from their male product. These androspores swarm for a time and finally settle down upon female filaments or even upon oogonia, where they become anchored and each produces a filament of a few cells, whose small



FIGS. 80–82. — *Oedogonium:* 80, contents of oospore escaping from the heavy wall in germination; 81, four zoospores forming in oospore; 82, the four zoospores completed. — After JURANYI.

form. It belongs to the fresh waters and is found attached to the leaves and stems of various aquatics, as water lilies, etc. The body is a flat thallus, being either a complete disk composed of radiating rows of cells (fig. 84) or a cushion with free branches. The zoospores are solitary, biciliate, and may be produced by any vegetative cell (fig. 89). In the discoid species the antheridia are formed by the division of a vegetative cell into four cells, each one of which produces a biciliate sperm (figs. 85, 86). In the branched forms, the antheridia appear as special club-shaped cells at the ends of branches. In the discoid forms the oogonia are near the ends of the radiating rows of vegetative cells, differing from them chiefly in size (figs. 84, 87). In the branched forms, the oogonia are free at the ends of branches, each developing a long tubular prolongation through which the sperm enters.

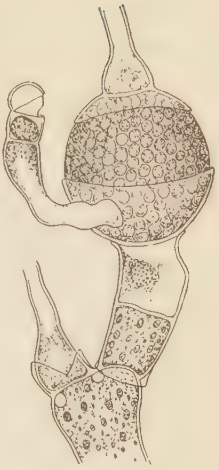


FIG. 83. — *Bulbochaete:* showing a dwarf male filament, with its terminal antheridium, attached to an oogonium. — After PRINGSHEIM.

Fertilization results not only in a thick-walled oospore, but in the branched forms contiguous cells of the thallus send out branches which invest it in a cellular case, making a sort of spore case (sporocarp), which is the resting stage of the plant. In germination the oospore gives rise to a several-celled body, each cell of which produces a zoospore that escapes and develops a new thallus (fig. 88).

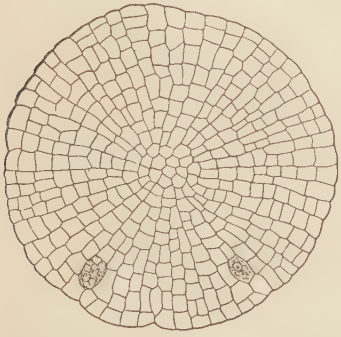
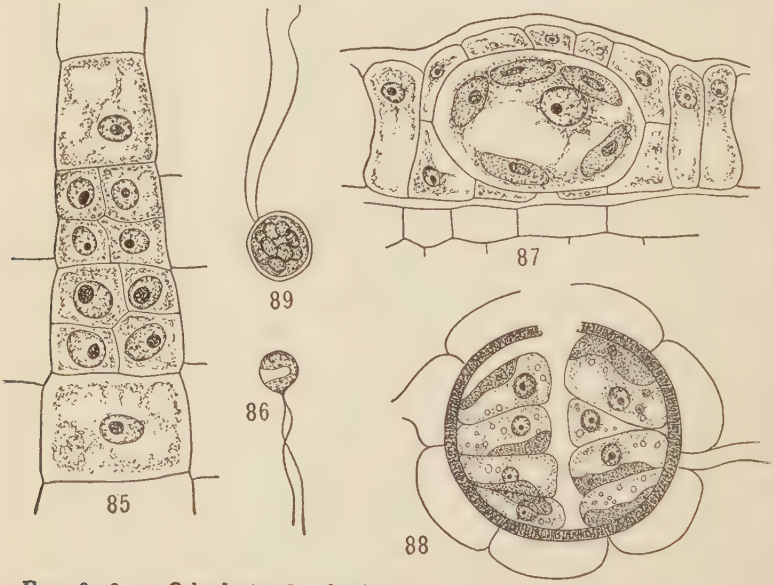


FIG. 84. — *Coleochaete scutata:* discoid form; the two larger and shaded cells are developing as oogonia.

Alternation. — Two noteworthy facts in this life history are the formation of a case of sterile cells about the oospore as a result of fertilization, and the multicellular body produced by the oospore. This last fact has been taken to represent the *alternation of generations* which is established as a constant feature of the higher plants. This phenomenon consists of the alternation of a sexual and a sexless generation in a life cycle, each generation giving rise to the other. In *Coleochaete* it was supposed that the sexual generation

(*gametophyte*) is represented by the ordinary gamete-producing plant, and the sexless generation (*sporophyte*) by the spore-producing body developed by the oospore. In subjecting this life history to what is regarded as a critical test of the two generations, it has been discovered that this special spore-producing body is not a sporophyte. The test has to do with the number of chromosomes in the nucleus, a number which is definite for each plant species. The chromo-



FIGS. 85–89. — *Coleochaete:* 85, development of antheridia, by the division of a vegetative cell into four cells; 86, a sperm (after PRINGSHEIM); 87, an oogonium, containing an egg showing nucleus and chloroplasts; 88, the heavy-walled oospore, invested by a jacket of sterile cells, and producing a multicellular body each of whose cells produces a zoospore (after OLTMANNS); 89, a zoospore (after PRINGSHEIM).

somes are doubled in number by the fusion of the sperm and egg to form the oospore; and this means that at some other point in the life cycle the number must be reduced again. Accordingly the sporophyte, which arises from the oospore, is characterized by the double or $2x$ number of chromosomes in its nuclei; and the gametophyte, which gives rise to the gametes, is characterized by the reduced or x number of chromosomes. Upon applying this test to *Coleochaete*, it was discovered that the special spore-forming body produced by the oospore contains the reduced number of chromosomes and is therefore not a

sporophyte. In fact, in this case, the doubling of chromosomes in the formation of the oospore is followed immediately by their reduction during the divisions of the oospore.

Conclusions. — Upon considering the assemblage of green algae here brought together under Confervales, the following general statements may be made: The body is a simple filament, a branching filament, or a flat thallus, and is either completely septate or partially coenocytic. Zoospores are produced abundantly, and are generally biciliate, *Oedogonium* being a notable exception. The sexual reproduction ranges from isogamy to a stage of heterogamy in which distinct oogonia and antheridia are developed. The zygospores may give rise directly to new plants or may produce zoospores; but the oospores always develop zoospores, a process which culminates in *Coleochaete* in a specially organized zoospore-producing body.

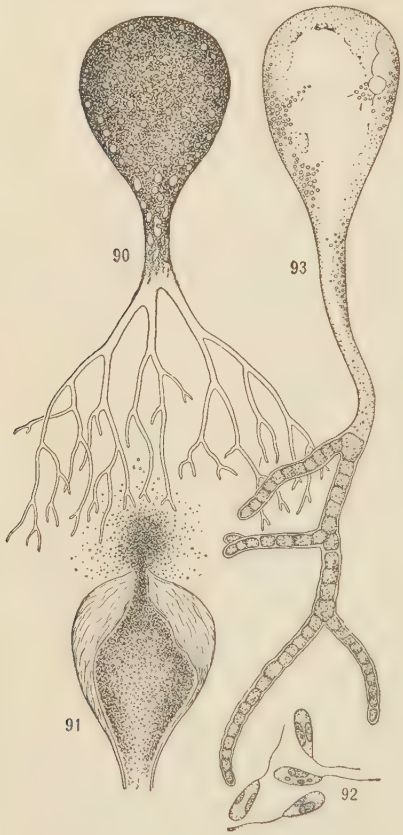
(d) Siphonales

General character. — This is a very well-defined group, comprising mostly marine forms. The distinguishing character, suggested by the name, is that the plant body has no cross walls, being one continuous multinucleate protoplast enclosed by the peripheral wall, a kind of body called coenocytic. In this case the body is completely coenocytic, as distinguished from such partially coenocytic bodies as those of *Cladophora* and *Sphaeroplea*. The bodies are more or less diffusely branching, and in some of the marine forms the differentiation of the body is remarkable, as in *Bryopsis*, *Caulerpa*, *Acetabularia*, etc. The two prominent fresh-water forms are as follows.

Botrydium. — This interesting plant develops in damp places, such as the mud of drying-up ponds, wet plowed ground, boggy fields, and especially on flood plains. It appears as groups of little green, balloon-shaped bladders, about the size of a pin's head, which grip the substratum by means of colorless, rhizoidal branches (fig. 90). Numerous small nuclei are embedded in the thin wall layer of cytoplasm, and in the aerial part there are numerous chloroplasts.

The asexual methods of reproduction are various, dependent upon varying conditions. A new bladder may bud out from the aerial part, send rhizoidal branches into the substratum, and then become separated from the parent by a wall. If covered with water, the whole inflated aerial portion may be converted into a sporangium producing a multitude of uniciliate zoospores (figs. 91, 92). These zoospores germinate

immediately upon damp earth, but if under water, they form a double wall and become resting spores. When the aerial portion of the plant is exposed to drought, the contents retreat into the protected rhizoidal branches and round off into a large number of non-motile spores (*aplanospores*), which rest until the return of favorable conditions and then initiate new plants (fig. 93). The development of aplanospores is common among algae, being a method used by the protoplast of bridging over unfavorable conditions, in which connection it appears more as a method of self-preservation than of reproduction. The aplanospores in germination give rise to new plants directly or to zoospores.



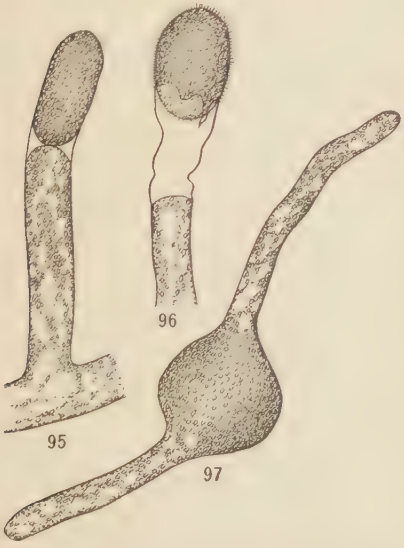
FIGS. 90–93. — *Botrydium:* 90, the ordinary vegetative form, showing the aerial green portion and the subterranean rhizoidal portion of the coenocytic body; 91, aerial portion of the body converted into a sporangium; 92, zoospores; 93, the formation of aplanospores in the rhizoidal region. — After ROSTAFINSKI and WORONIN.

The testimony in reference to the sexual reproduction of *Botrydium* is conflicting. It has been stated that the aplanospores give rise to numerous small biciliate gametes that conjugate, but it is claimed that the gametes observed are those of *Protosiphon*, a form which grows with *Botrydium* and closely resembles it. In any event, the presence of gametes among these simpler Siphonales is the important point for our purpose, and it is of interest to note that they either conjugate or germinate as small zoospores.

Vaucheria. — This is the very common green felt, which occurs in coarse feltlike masses of branching filaments on damp soil and in fresh or brackish water (fig. 94). As in all coenocytic bodies, the nuclei and chloroplasts are numerous, and in this form oil-globules are abundant.

Zoospore. — The asexual reproduction is modified in an interesting way by the coenocytic habit. At the tip of a branch a very large zoospore is formed by the protoplast, and is cut off from the general body by a wall (fig. 95). It is discharged through an opening at the end of the branch and moves actively by means of cilia that are distributed over its whole surface (fig. 96). The zoospore is multinucleate, containing the nuclei that were in the end of the branch at the time of its formation, and in connection with each nucleus a pair of cilia is formed. This large zoospore, therefore, may be regarded as a compound zoospore, corresponding to a number of biciliate zoospores. It germinates directly, producing a new filament (fig. 97).

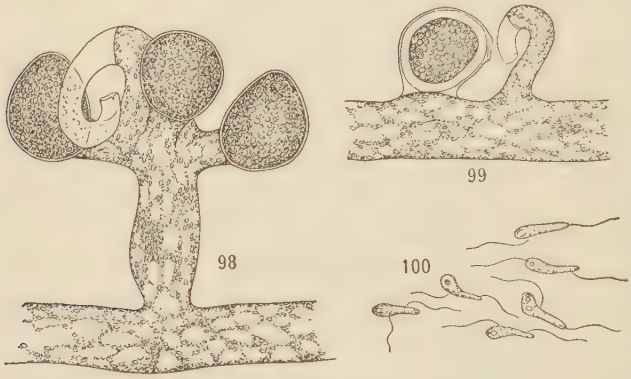
FIG. 94. — *Vaucheria:* a small portion of the filamentous, branching, coenocytic body.



FIGS. 95–97. — *Vaucheria:* showing formation (95), escape (96), and germination (97) of zoospore. — After COULTER.

Sexual reproduction. — The structures connected with sexual reproduction are more highly developed than any previously mentioned, for not only is *Vaucheria* heterogamous, but it produces special sex organs which are not transformed vegetative cells, but are specifically for gamete-production from the beginning. In one of the species, for example (fig. 99), a special branch is put out from the side of the filament, and a terminal cell is cut off by a wall and enlarges into a more or less globular oogonium, in which a single large egg (oosphere) is formed. This egg at first is multinucleate, but

after the partition wall is formed, it becomes uninucleate by the degeneration of the other nuclei. In the wall of the oogonium a more or less beaked opening is formed by which the sperms enter. The antheridial branch is similar in origin, but is longer, the antheridium being cut off at the curved tip by a wall as a small cell. In other species a single sexual branch bears both oogonia and antheridia (fig. 98), a common arrangement of the cluster being a terminal antheridium and a group of laterally developed oogonia. In each



FIGS. 98–100. — *Vaucheria:* 98, 99, two methods of forming oogonia and antheridia; in both cases the terminal antheridium has discharged its sperms (100). — 100, after WORONIN.

antheridium numerous sperms are formed (fig. 100), which are discharged, enter through the beaked openings of the oogonia, and fertilize the eggs. The heavy-walled oospore is the protected stage of the plant and germinates directly into a new filament.

Experiments. — The experiments upon *Vaucheria* are of great interest, since by varying the character of the medium, the nature of the nutrition, the light, etc., there may be produced at will sterile plants, zoospore-producing plants, or gamete-producing plants. *Vaucheria* also has great power of resisting unfavorable conditions, in the presence of which the filament becomes chambered by the formation of thick cross walls, and the contents of each compartment round up as an aplanospore. In favorable conditions each aplanospore either forms a new filament directly, or discharges an amoeba-like protoplast, which rounds off as a green sphere, covers itself with a wall, and either forms a filament directly or enters again into a period of rest. This ability to respond promptly to varying conditions and to change the program at almost any period in the life history is very marked among the lower plants.

Conclusions. — The body of Siphonales is coenocytic and usually complexly branched and differentiated. Zoospores are formed, which sometimes take on the character of the coenocytic body and may be regarded as compound zoospores, as in *Vaucheria*. Sexual reproduction ranges from isogamy to heterogamy, in the latter condition extending to the formation of special branches bearing the sex organs. Aplanospores or non-motile protected cells are produced under conditions unfavorable for vegetative activity, and from all spores or resting cells there is a direct development of new filaments. A possible connection of Siphonales with Confervales is suggested by such partially coenocytic forms as *Cladophora* and *Sphaeroplea*, but in any event it is to be regarded as a highly specialized group.

(e) Conjugales

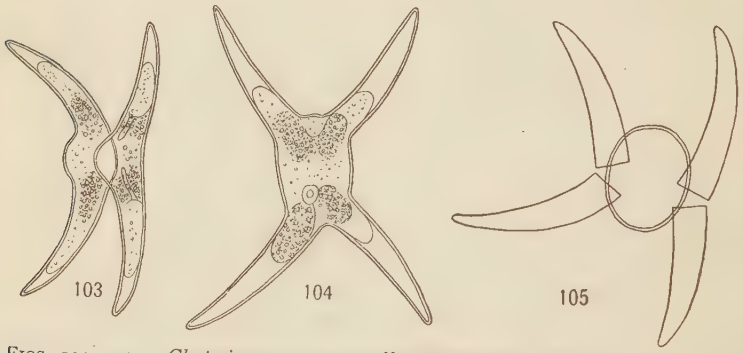
General character. — This is also a very distinct group, which is separated by some writers from Chlorophyceae on account of its peculiar features. It is a fresh-water group, the bodies being single cells or simple filaments, and characterized by remarkable chloroplasts, by the absence of swimming spores, and by a peculiar method of sexual reproduction. The absence of all ciliated cells, including both spores and gametes, in an aquatic group is remarkable. The following families may be used to illustrate the group.

Desmidiaceae. — The desmids are one-celled plants that exhibit the greatest possible variety of form and are often extremely beautiful. The cell is peculiar in being organized into two symmetrical halves, often separated by a deep constriction which makes the *isthmus*. In each half there is a large, irregular, often complex chloroplast and several pyrenoids, while in the isthmus connecting the two halves the single nucleus is placed. Many of the desmids can move about, and they are very sensitive to light, taking a position determined by the incident rays.

FIGS. 101, 102. — *Closterium:* 101, cell dividing, the two nuclei and the wall having been formed; 102, the plastid in an old "half cell" having divided, and the nucleus becoming placed between the two plastids. — After A. FISCHER.

Individuals are multiplied by cell-division. The nucleus divides and a wall is formed across the isthmus (fig. 101). The division thus results in two new cells, each consisting of one half of the old cell and a portion of the isthmus, which enlarges into a new half, when the two cells separate. During this process the plastid in each half divides, so that the new cell contains the usual two plastids (fig. 102).

In sexual reproduction the cells pair, the walls are ruptured at the isthmus, the protoplasts escape and fuse, and a zygospore is formed (figs. 103–105). In some species a little tubular projection puts out from



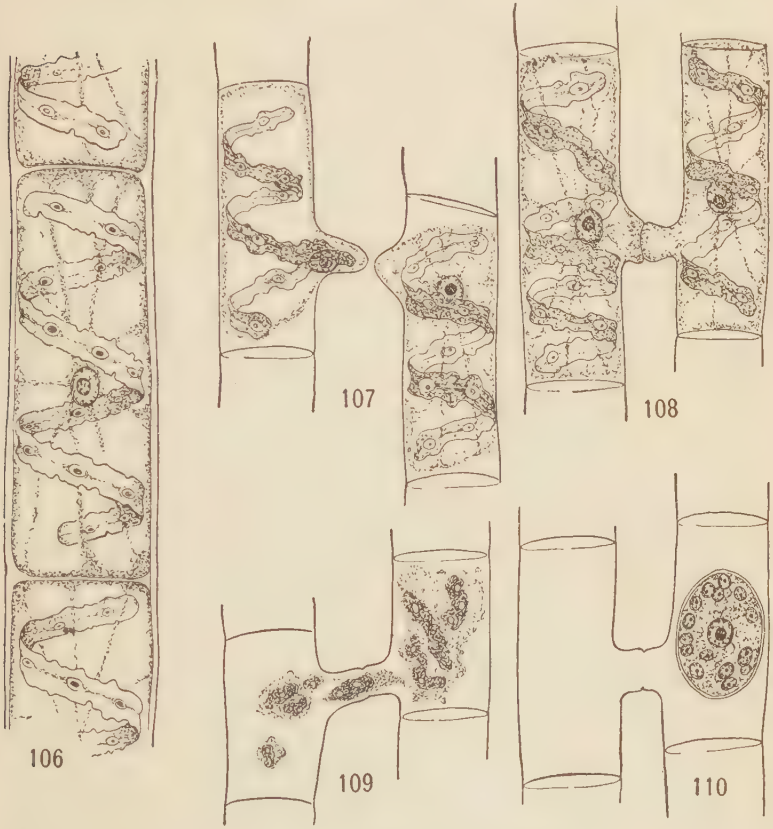
FIGS. 103–105. — *Closterium:* 103, two cells pairing for conjugation; 104, the two protoplasts fusing; 105, the zygospore formed. — 103, 104, after DE BARY; 105, after WEST.

each cell at the isthmus, and the two projections meet to form a short tube in which the protoplasts meet and fuse. The sexual fusion in desmids is true conjugation, in which two vegetative protoplasts fuse without the organization of distinct gametes. In the germination of the zygospore the heavy wall is ruptured, the protoplast escapes, and four nuclei are formed, only two of which usually persist in the development of new desmids.

Mesocarpaceae. — In this family the body is a filament of similar elongated cells, in each of which there is an axial platelike chloroplast. Cell division is accomplished by nuclear division and a centripetally growing wall. Sexual reproduction occurs between adjacent filaments, whose cells pair and come in contact by kneelike bends or by short tubes, and the two abutting walls becoming perforated at their contact, permit the two similar protoplasts to come in contact for fusion. The zygospore upon germination forms a new filament directly.

Zygnemaceae. — These are pond scums, and are among the most common of the green algae. The characteristic genera are *Zygnema*

and *Spirogyra*, the latter being especially abundant and long used for laboratory study. They are both filamentous plants with elongated cells, and differ from one another in the form of the conspicuous chloroplasts, which in *Zygnema* are two radiate or starlike bodies in each cell

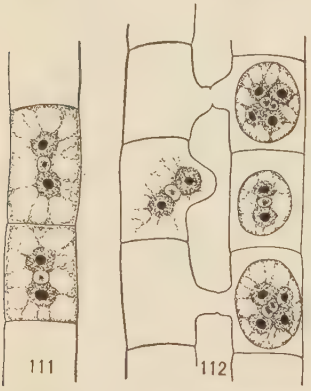


FIGS. 106–110. — *Spirogyra:* 106, cell showing the spiral bandlike chloroplast containing pyrenoids, and the centrally swung nucleus; 107, cells developing a conjugating tube; 108, conjugating tube complete; 109, passage of one protoplast through the tube; 110, the zygospore. — After COULTER.

(fig. 111), and in *Spirogyra*, one or more bands that extend spirally from one end of a cell to the other (fig. 106). *Spirogyra* may be selected to represent the family. The conspicuous green, spiral, bandlike chloroplasts lie peripherally in the cell and contain conspicuous, nodule-

like pyrenoids, which are often surrounded by a starch jacket. The nucleus is swung in the center of the vacuolate cell by strands of cytoplasm that connect the sheath of cytoplasm about the nucleus with the peripheral layer of cytoplasm. The cell division is as described for the Mesocarpaceae.

Sexual reproduction. — Sexual reproduction is most characteristic (figs. 107–110, and fig. 112). Conjugating tubes put out from the cells of adjacent filaments and fuse, until the two filaments connected by conjugating tubes resemble a ladder. The protoplast of one cell passes through the conjugating tube into the connected cell, and the two protoplasts fuse, forming a large, heavy-walled zygospore. The conjugating protoplasts in this case differ in behavior, one being passive and the other relatively active, so that there is apparent a distinction of sex, although the two protoplasts are similar in appearance. This distinction often extends to the filaments, one filament emptying all of its protoplasts into the cells of the connected filament; in which case the former filament can be regarded as male and the latter one as female. It is very common to see a filament, all of whose cells are empty, connected with another filament, each of whose cells contains a zygospore. On the other hand, the same filament may give and receive protoplasts; and in some species conjugating tubes connect adjacent cells of the same filament. Occasionally, also, bodies which resemble zygospores are found within cells that have established no connections, and so they have been formed without fusion, a phenomenon called *parthenogenesis* (fig. 112). Great variations in the establishment of connections for conjugation may be found in almost every collection of zygospore-forming material. The zygospore is the winter condition of the plant, and upon germination gives rise directly to a new filament.



FIGS. 111, 112. — *Zygnema:* 111, cells showing the two radiating chloroplasts, between which is the nucleus; 112, conjugation, showing two zygospores (each with two nuclei and four chloroplasts) formed by the fusion of two protoplasts, and a third zygospore-like cell not formed by fusion (illustration of parthenogenesis).

Conclusions. — The body of the Conjugales consists of a single cell or a simple filament, and in its vegetative phase is distinguished by large

and characteristically shaped chloroplasts. There is no reproduction by motile spores, and no motile cells of any kind are formed. Sexual reproduction is effected by the conjugation of protoplasts brought together usually through conjugating tubes, and while in a general way only isogamy is attained, there is evident in some forms an incipient heterogamy shown by the different behavior of the pairing protoplasts. The group as a whole seems to stand stiffly apart from all those previously considered, and must be regarded as very highly specialized.

(f) Charales

General character. — The stoneworts, as these forms are called, constitute a very isolated group among thallophytes, which seems to hold no definite relation to any other group. If they are algae, they must be included among the green algae; but they are considered by many to be quite separate from algae; and some would even remove them from thallophytes. Until something more is known of their relationships, however, it is convenient to consider them in connection with the green algae. They are found in fresh and brackish waters, attached to the bottom and covering large areas with a dense mass of vegetation. Some of the bodies are incrusted by such an abundant deposit of calcium carbonate that it makes them rough and brittle, and suggested the name stoneworts. The common genera are *Chara* and *Nitella*, and the general structure is very uniform.

FIG. 113. — *Chara*: showing general habit of body.

Vegetative body. — The vegetative body consists of a cylindric stem or main axis which branches profusely (fig. 113). All of the axes are differentiated into short *nodes* and long *internodes*, and from the nodes the

whorls of branches arise. These branches are of two kinds: (1) those of limited growth, the so-called "leaves"; (2) those that resemble the parent axis in indefinite growth. The branches of limited growth form the whorl or rosette of branches at each node; while usually in the axil of one of them the branch of indefinite growth appears. The axillary position of the main branch suggested that the smaller subtending branches are leaves.

The main and lateral axes elongate by means of an apical cell (fig. 114), which by successive transverse walls cuts off a longitudinal series of cells (segments). Each segment divides transversely into two cells, the lower one of which enlarges, forming the long internodal cell (sometimes 10 cm. or more long), the upper one giving rise by successive divisions to the plate of nodal cells, which develop the branches. In *Nitella* the long internodal cells remain uncovered; but in *Chara* they become covered by a sheath of cells developed from the basal cells of the short branches, so that a cross section of an axis shows a central cell of large caliber sheathed by a ring of small cells (cortical cells). The protoplast of the internodal cell consists of a thick peripheral layer of cytoplasm surrounding a large central vacuole and embedding numerous nuclei and oval chloroplasts. In a young internodal cell there is a single large nucleus, but in connection with the great enlargement of the cell the nucleus gives rise to numerous nuclei by fragmentation. The internodal cells of *Nitella* are noteworthy for exhibiting streaming movements of protoplasm with remarkable distinctness.

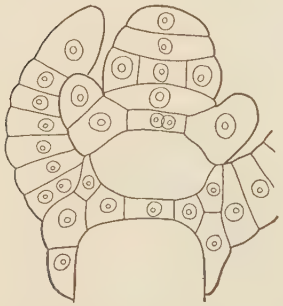
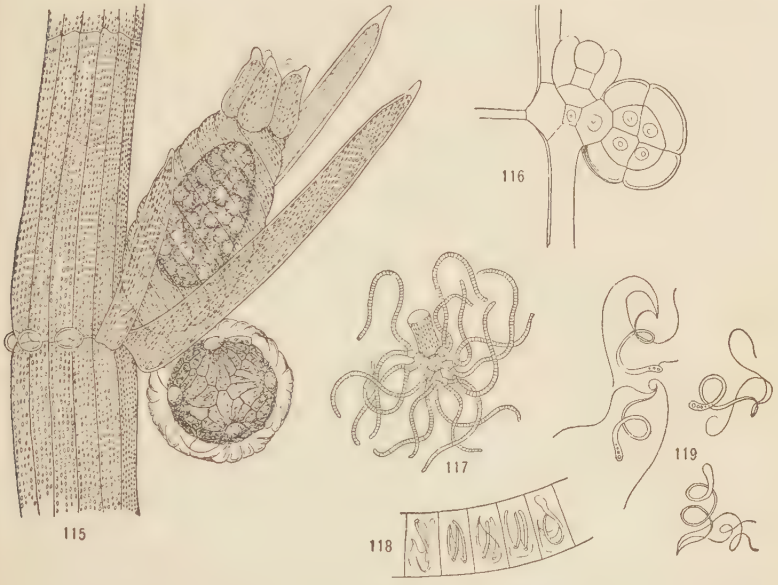


FIG. 114. — *Chara*: apical cell cutting off segments to form nodes and internodes; the nodal cells forming branches. — After SACHS.

Reproduction. — No asexual spores are produced, but vegetative multiplication is secured by tuberlike outgrowths, special branches, etc., from the nodes. The structures connected with sexual reproduction, however, afford the most distinguishing feature of the group. The antheridia and oogonia, instead of being single cells, as in the groups previously described, are highly complex structures. They are borne at the nodes of the short branches and are visible to the naked eye, the mature antheridia being deep orange to red (fig. 115).

Antheridium. — The antheridium is globular, the wall being com-

posed of eight triangular, platelike cells known as *shields* (fig. 115). Projecting centripetally from the center of each shield is an elongated cell (*manubrium*), which bears a terminal cell (*head cell*). These head cells give rise to a varying number of similar cells, and each ultimate cell produces a pair of long filaments, each consisting of approximately 200 cells, each cell producing a single sperm (figs. 117, 118). The interior of the antheridium, therefore, is a tangle of filaments, and the



FIGS. 115–119. — *Chara:* 115, branch bearing oogonium (showing its sterile jacket and crown) and antheridium (showing its interlocking, shieldlike wall cells); 116, young oogonium (stalked and not yet completely invested by the jacket) and antheridium; 117, manubrium bearing head cells and sperm-containing filaments; 118, detail of cells of filament showing contained sperms; 119, sperms (spirally coiled and biciliate). — After SACHS.

sperm output of a single antheridium may range between 20,000 and 50,000. The sperm is a more specialized structure than is the zoospore-like sperm of the ordinary algae, and more resembles the sperms of higher plants. The nucleus with its sheath of cytoplasm forms the *body;* the cytoplasm extends to form an elongated more or less spirally coiled *beak*, and from its tip two long cilia are produced (fig. 119).

Oogonium. — The oogonium, which replaces a secondary branch, is an enlarged apical cell, and produces a single large egg filled with starch

grains and oil drops. The complexity arises from the fact that the oogonium is closely invested by spirally wound elongated cells that arise from the cell beneath. Above the oogonium each investing cell cuts off a tip cell, the cluster of tip cells forming the so-called *crown* (figs. 115, 116). In fertilization the crown cells spread apart at the base, leaving five small slits, through which the sperms pass. Upon the formation of the oospore, the walls of the envelope cells thicken and harden, forming a nutlike spore case, which is the resting stage. Upon germination, the oospore sends out a simple filament and an elongated rhizoidal cell, a structure called the *proembryo*, and from the proembryo the adult shoot arises as a lateral branch. The adult plants, therefore, arise as lateral branches from a very different body.

Conclusions. — It is evident that the Charales cannot be related to the other green algae, since they differ strikingly in vegetative body, sex organs, sperms, and life history — in all of which particulars the resemblances are rather with the higher plants. They should at least be isolated as a distinct group of Thallophytes, or preferably should constitute a group between Thallophytes and Bryophytes.

(2) Phaeophyceae

General character. — The brown algae are almost all marine. They occur on all seacoasts, but are more abundant and conspicuous in the cooler waters. The forms exposed to tidal action have tough, leathery, and firmly anchored bodies, which sometimes reach such dimensions as hundreds of feet in length. They are also often highly differentiated, both as to form and tissues. The nature of the characteristic pigment or pigments is in doubt. The green constituent may or may not be chlorophyll, but in any event there are also present certain brown or yellow constituents which give the characteristic color to the plants, referred to in the name of the group. It must not be supposed that all brown algae are necessarily brown, for there are gradations in the hue of the bodies from brown to olive green, but the characteristic brown or yellow constituents are always present. Two of these constituents have been separated and named *phycoxanthin* and *phycophaein*. Another general character of brown algae is that all the motile cells (zoospores and sperms) are laterally biciliate, in sharp contrast with the apically ciliate cells of most algae.

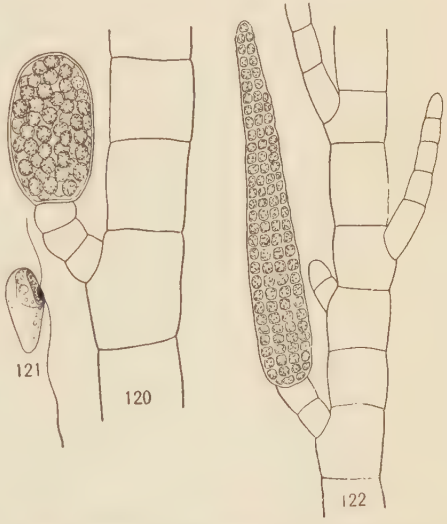
The group is regarded as a highly specialized one, giving little or no indication of its origin. There is certainly no indication that it has

been derived from the Chlorophyceae, and it has possibly developed independently from such organisms as gave rise to the green algae. None of the true brown algae are one-celled, the simplest being a simple conferva-like filament, and the group also includes forms with very complex bodies. Sexual reproduction is probably present in all the forms, having been discovered recently in *Laminaria*, and is chiefly represented by isogamy, but a small group has attained heterogamy.

The two orders of brown algae are distinguished by their methods of reproduction: *Phaeosporales*, characterized by the formation of zoospores and by prevailing isogamy; *Fucales*, characterized by the absence of zoospores and by well-developed heterogamy.

(a) Phaeosporales

General character. — This group includes the large majority of brown algae and also the most bulky. The zoospores and gametes are alike, and are produced in special organs — the *sporangium* and the *gametangium*. It will not be possible or profitable to give an account of the numerous families, but the general features of the group may be indicated by the following illustrations:



FIGS. 120–122. — *Ectocarpus:* 120, monosiphonous filament bearing a sporangium on a short lateral branch; 121, a zoospore, showing the laterally biciliate character (after KUCKUCK); 122, filament bearing a gametangium ("plurilocular sporangium").

Ectocarpus. — This form occurs as tufts of branching, many-celled filaments. The filament consists of a single row of cells, the body being called *monosiphonous*. If the body consists of several parallel rows of cells, as in certain other brown algae, it is called *polysiphonous*.

Sporangium. — The sporangium is a single cell, which in some forms is a cell of the filament changed in function and usually in size; and in other forms is developed at the end of a special short lateral branch (fig. 120).

In either case the zoospores produced are laterally biciliate (fig. 121) and develop new filaments directly.

Gametangium. — The gametangium is a many-celled structure, and, like the sporangium, is developed either from ordinary cells of the filament or at the end of a short lateral branch (fig. 122). The small cells composing it are cubical, being packed together closely, and each one produces a biciliate, zoospore-like gamete. Upon escaping, the gametes pair and fuse, and a zygospore is formed. This gametangium is of great interest on account of the variations that occur, leading sometimes to uncertainty as to whether the structure should be called a gametangium or a sporangium; in fact, it is often called a *plurilocular sporangium*, in distinction from the true *unilocular sporangium*. In some cases the gametangium is reported to produce both zoospores and gametes, judged by their behavior. The question might be raised whether the so-called zoospores in this case are not parthenogenetic gametes (see p. 40). Other cases are reported in which the gametangium is said to produce motile cells of three sizes, the medium-sized ones germinating directly, and the largest and smallest ones pairing. In this case, we should have not only zoospores, but also dissimilar gametes. In another case it is reported that the larger gamete comes to rest and is fertilized in this quiescent condition; in which case heterogamy would be very apparent. In the same genus, therefore, there occur both zygospore and oospore formation, and more or less confusion of gametes and zoospores. The group would seem to be an unusually favorable one for observing both sex origin and sex differentiation.

FIG. 123. — *Laminaria:* showing bladelike body, stipe, and holdfast.

Sphacelaria. — In general structure and reproductive habits this form resembles *Ectocarpus*, but it may be used to illustrate the appearance and powers of an *apical*

cell. In such filamentous bodies as were met among the green algae, the filament is elongated by the division of all the cells; in other words, the power of cell division is distributed throughout the filament. In *Ectocarpus* this power of cell-division to elongate the filament is more restricted, often being specially present in a region behind the tip, where the divisions occur in unusually rapid succession. In *Sphacelaria* this special power has become restricted to the apical cell, which in this case is often extraordinarily large. It cuts off a succession of cells that adds to the length of the filament, and after each division it enlarges again. This does not mean that other cells do not have the power of division, but that all the cells are descendants of the apical cell. An apical cell, therefore, is not merely the cell at the apex, but a cell in that position which has the power of giving rise to the succession of cells that organizes the plant body.

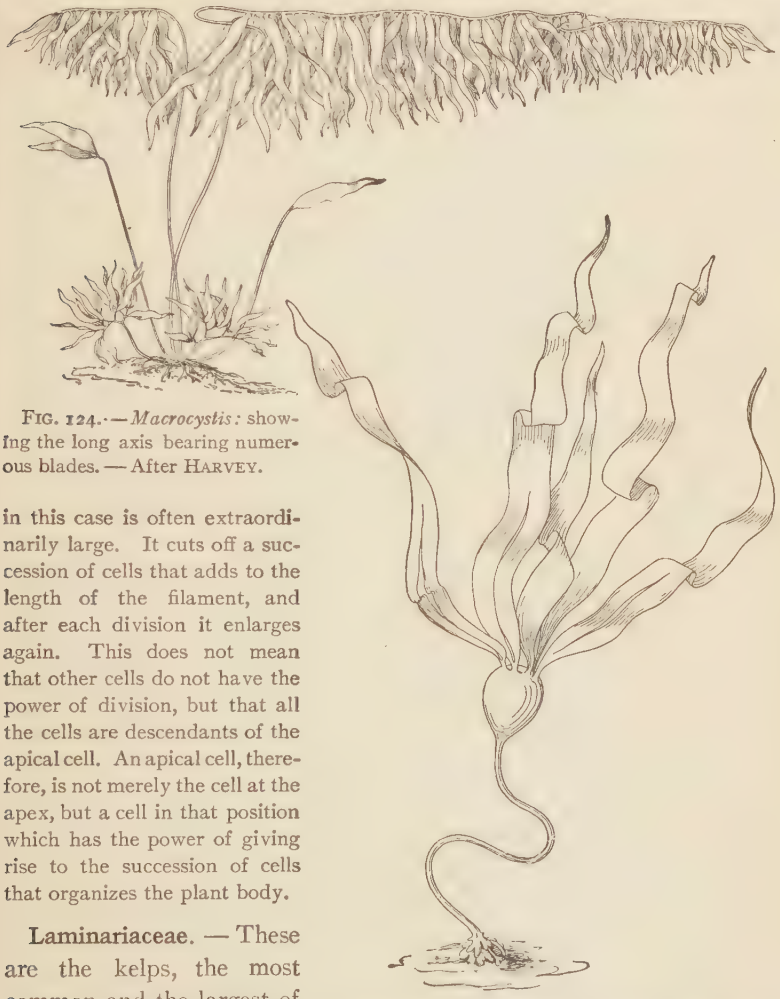


FIG. 124. — *Macrocystis:* showing the long axis bearing numerous blades. — After HARVEY.

FIG. 125. — *Nereocystis:* showing the blades arising from the bladder-like expansion of the tip of the stipe.

Laminariaceae. — These are the kelps, the most common and the largest of the brown algae. They are common on rocky coasts,

being most abundant in northern latitudes. In the North Atlantic the large forms are chiefly species of the *Laminaria* type, the body resembling a huge leathery and stalked leaf blade sometimes 9 to 10 m. long, anchored by a rootlike holdfast (fig. 123). The most remarkable forms, with variously arranged blades, occur on the Pacific coast, among them being *Macrocystis* (giant kelp), whose huge bulk sometimes extends 200 to 275 m. (fig. 124); *Nereocystis* (bladder kelp), with long flexible stem (reaching 60 m.) that swells at the end into a large globular float to which are attached large blades (fig. 125); *Lessonia*, with a dichotomously branching stem like a tree trunk; and *Postelsia* or sea palm, whose name suggests its habit (fig. 126).

FIG. 126. — *Postelsia* (sea palm): showing numerous blades from the massive stipe, and the system of holdfasts.

The bodies are differentiated into blade, stipe (sometimes extremely long), and holdfast. The holdfast often takes the appearance of an excessively branching and very tough root system, but it should not be confused with roots in either structure or function. There is also often a marked differentiation of the cells into distinct tissues. For example, a section of the stipe of *Nereocystis* shows an outer pigment-bearing zone (cortex), a zone of storage cells, and a pith region (medulla) of loosely woven elongated cells. Although often very large and complex in form and tissues, the kelps, so far as known, are very simple in their reproductive methods. The gametangia occur in dense masses on certain portions of the ordinary

blades or on special blades, and the gametes which they produce were formerly mistaken for zoospores. It seems probable that zoospores have been eliminated from the life history of the kelps, as in the Fucales, and that the only spores are zygospores.

Cutleriaceae. — The body in this family is a broad, flat, forking thallus, and zoospores are formed as in other Phaeosporales; but there is a differentiation of gametes that deserves attention. Gametangia of two kinds are produced, similar in appearance, but dissimilar in gametes. One kind of gametangium produces fewer and larger gametes, the other more numerous and smaller gametes, and both kinds are ciliated and set free. In such a case, the two kinds of gametangia may be regarded as multicellular oogonia and antheridia, the fusion as fertilization, and the product as an oospore. Cutleriaceae, therefore, may be taken to represent a transition from Phaeosporales to Fucales.

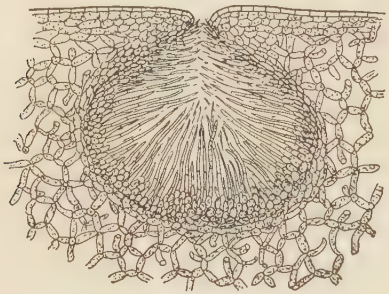
(b) Fucales

General character. — This relatively small and specialized group of brown algae is characterized by the absence of zoospores and the presence of well-developed heterogamy. The common representatives are *Fucus* (rockweed) and *Sargassum* (gulfweed).

Fucus. — The body of these exceedingly common forms is a flat thallus which forks repeatedly (fig. 127), a type of branching called *dichotomous*. It grows by means of an apical cell, which soon becomes placed at the bottom of a notch by the more rapid growth of the two branches. The body is attached to its support by a basal disk, and is made buoyant by air bladders or floats that are inflated intercellular spaces. There is also a distinct differentiation of tissues into the more compact cortex and the looser medulla. The absence of zoospores in an aquatic form or of asexual spores of any kind is hard to understand.

FIG. 127. — *Fucus:* showing the dichotomous thallus, the region of sex organs at the branch tips, and the air bladders.

Sex organs. — In the thallus body, often at the tips of special branches, there occur the *conceptacles*, which are chambers, each of which opens to the surface by a small porelike opening. Within these conceptacles the antheridia and oogonia are produced, the two organs appearing in the same conceptacle or in different ones (figs. 128, 129). The conceptacles contain also numerous branching filaments (*paraphyses*), which



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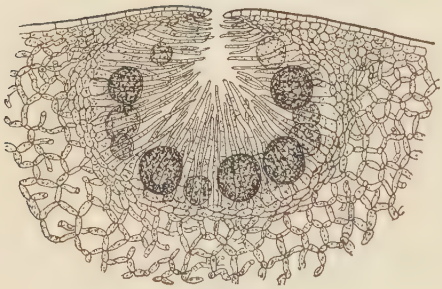

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FIGS. 128, 129. — *Fucus:* 128, an antheridial conceptacle; 129, an oogonial conceptacle. — After THURET.

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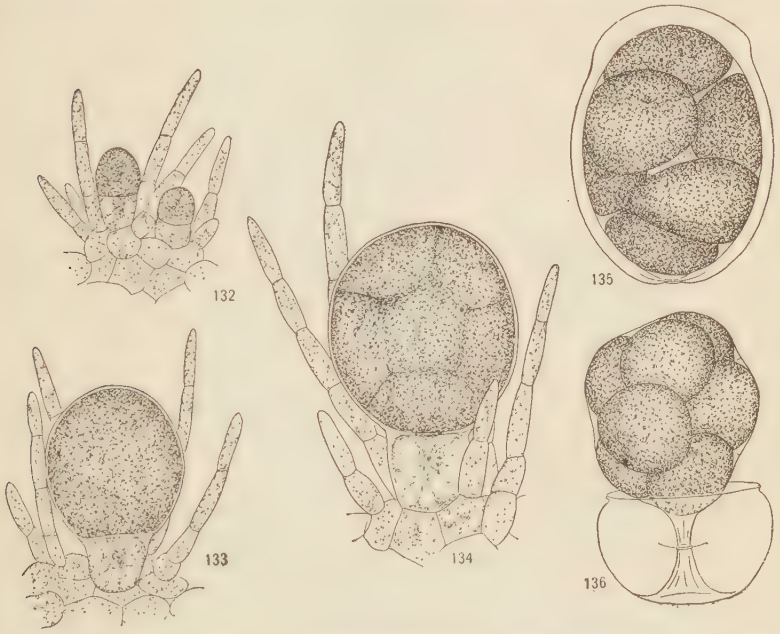
FIGS. 130, 131. — *Fucus:* 130, the oval antheridia borne on a branching paraphysis; 131, the laterally biciliate sperms. — After THURET.

arise from the cells bounding them. The antheridia are borne as lateral branches of these paraphyses and are produced in great profusion (figs. 130, 131). They are oval cells that produce numerous small laterally biciliate sperms. The oogonium is a large, globular, stalked cell and commonly produces eight eggs (oospheres) (figs. 132–136). There are related genera whose oogonia produce four or two eggs, and often only one; but in all of them eight nuclei appear. Such evidence suggests

that the forms with one, two, or four eggs have been derived from those with eight, some of the eggs not developing, but all eight represented by nuclei. Both sperms and eggs are discharged and escape from the conceptacle. *Fucus* is remarkable, therefore, not only in the production of eight eggs by the oogonium, but also in the fact that they are discharged before fertilization. The eggs float and are surrounded by



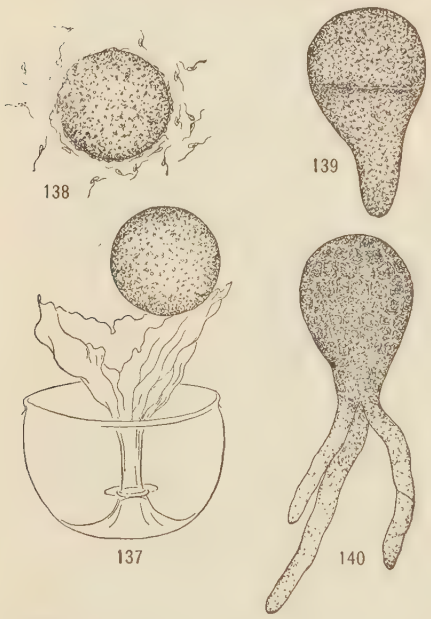
FIGS. 132–136. — *Fucus:* 132, young oogonia among the paraphyses; 133, an older oogonium; 134, oogonium beginning to develop the eight eggs; 135, the eggs rounded off; 136, the eggs escaping from the oogonium. — After THURET.

swarms of sperms, which have been observed to set them rotating (figs. 137, 138). The functioning sperm enters the egg, comes in contact with its nucleus, and the two nuclei lying in contact gradually fuse. Apparently the oospore is not a resting cell, but develops a new plant at once (figs. 139, 140).

In following the life history of *Fucus* it has been found that the number of chromosomes, which is doubled by the fusion of the male and female nuclei, is not reduced until the gametes appear. Therefore, using the number of chromosomes as a test, the whole vegetative plant is the

sporophyte generation (the one with $2x$ chromosomes), and the gametophyte (the x generation) is represented only by the gametes.

Sargassum. — The gulfweeds are well known on account of their connection with the so-called Sargasso Sea. In that great ocean eddy, these gulfweeds accumulate in vast quantities, and the impression has been that they have been torn from the coast and swept out to sea. In any event, they continue growing, and perhaps pass through their whole life history in this floating condition. They are remarkable for the differentiation of the body into regions which may well be called leaves and branching stems, and they also produce short branches that develop the bladder-like floats which resemble small berries (fig. 141). So far as is known, the reproduction resembles that of *Fucus*.



FIGS. 137–140. — *Fucus:* 137, an egg freed from the oogonium; 138, an egg surrounded by a swarm of sperms; 139, a fertilized egg beginning to germinate; 140, a young plant. — After THURET.

In connection with the brown algae, it is convenient to consider two groups of thallophytes whose connections are entirely uncertain. It must be understood that they are not presented as brown algae, or as algae at all.

Diatoms. — This is a vast assemblage of one-celled plants that occur in profusion in fresh and salt water and damp soil. They exist in such tremendous numbers in the ocean as to form a large part of the floating *plankton*, that free-swimming and free-floating world of minute organisms. Many diatoms occur as fossils, forming large deposits, as the so-called siliceous earths, etc. They are solitary and free-swimming forms, or are attached by gelatinous stalks excreted by the cells, the stalks often profusely branching. The forms of the cells are too numerous for description, a common free-swimming form being boat-shape (*Navicula*), but there are rods, wedges, disks, etc. (figs. 142–145).

Cell wall. — The cell wall is a special feature, for it consists of two siliceous valves, one overlapping the other, like the two parts of a pill box. The wall is so impregnated with silica that it forms a complete and resistant siliceous skeleton.

In many cases the valves are sculptured with fine transverse lines (really rows of dots), the markings being so regular and minute as to serve as a test of the definition of lenses. There is also a longitudinal line (*raphe*), which represents a cleft or a series of openings through which pseudopodia are thrust for locomotion. There are two distinct aspects of such cells: that showing the relation of the valves being the *girdle* side and that showing the face of a valve being the *valve* side.

Structure. — The protoplast consists of usually peripheral cytoplasm, a central nucleus swung in a bridge of cytoplasm, and two large or numerous smaller brownish yellow chromoplasts, often called *endochrome plates*. Their color is due to the

FIG. 141. — *Sargassum:* showing the appearance of stem and leaves, and the berry-like floats.

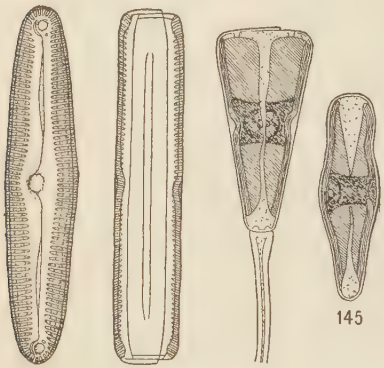
chlorophyll (at least a green constituent) and a characteristic golden brown constituent called *diatomin.*[1]

Cell-division and auxospores. — In cell-division the growth of the protoplast separates the valves, and division occurring in the plane of the valves, each new protoplast possesses one of the old valves and forms a new valve on the naked side. It is evident that one of the two cells thus produced has the same size as the parent cell; while the other cell is smaller, for the smaller valve of the parent cell becomes the larger (overlapping) valve of the daughter cell. This means that among the progeny cells there are series of individuals of diminishing size. When this diminution in size has reached a minimum, the *auxospores* are formed, the name indicating "enlarging spores." Auxospores may be produced in a variety of ways, the simplest being the separation of the valves and the escape of the protoplast, which in this free condition grows to the maximum size and develops new valves. In this case the auxospore is simply the escaped protoplast. In other

[1] The precise relation of these pigments is not certainly known.

cases the protoplast divides into two daughter protoplasts that escape and function as auxospores, the process suggesting real spore formation. Both of these methods are also associated with sexual reproduction: in the one case the escaped protoplasts of two contiguous cells conjugate to form the auxospore; and in the other case the four daughter protoplasts from two contiguous cells pair and conjugate. An auxospore, therefore, may be a naked protoplast, an asexual spore, or a zygospore, the feature in common being that there is a restoration of size before valve formation.

Relationships. — Such characters do not suggest any evident relationships for the diatoms, and they seem to stand apart from other groups of thallophytes, excepting perhaps the Peridineae (see below), and such a connection would not help the problem much. In certain particulars the cell structure suggests that of the desmids, and by some the diatoms are associated with them under Chlorophyceae (Conjugales). The brown pigment associated with the green suggests Phaeophyceae, and hence in some texts diatoms are found among the brown algae. It is perhaps best at present to keep the group apart from others, as one of the several unrelated groups of thallophytes.



FIGS. 142–145. — *Diatoms:* 142, free-swimming form, valve side; 143, same form, girdle side, showing the relation of the valves; 144, 145, girdle and valve views of a stalked form. — 142, 143, after PFITZER; 144, 145, after ENGLER and PRANTL.

Peridineae. — These organisms are mostly marine and are associated with diatoms in forming much of the plankton of the ocean. They consist usually of single cells which are naked or have a cellulose wall, which is often sculptured. The naked forms are laterally biciliate, thus resembling the zoospores of the brown algae. The nucleus is distinct; there is a complex system of vacuoles; and there may be green, yellow, or brown chromoplasts, or none at all; meaning that some forms have the food-manufacturing power of algae and others have not. Many of the forms multiply freely by ordinary cell-division, and sometimes there are regularly formed zoospores. No gametes are recorded, but it seems very probable that the free "zoospores" may sometimes conjugate. The characters given indicate a low synthetic group; for the ciliated vegetative cells suggest the simpler Volvocales; the sculptured walls, chromoplasts, and other features suggest diatoms; the laterally biciliate motile cells and yellow or brown chromoplasts suggest brown algae; and the forms without chromoplasts do not suggest algae at all.

(3) RHODOPHYCEAE

General character. — This great group, containing only a few fresh-water forms, includes the majority of the marine algae. They are by

no means so bulky as many of the brown algae, but they are much more diversified in form. In the simplest forms the body is a simple or branching filament, which is monosiphonous or polysiphonous (see p. 45), or it may be flat and filmy, or ribbon-like. The more complex forms show an extreme differentiation of the body into branching stems, leaves, and holdfasts. The species of *Corallina* resemble branching coral on account of the abundant deposit of calcium carbonate in their cell walls. The general hue of the plants is red or violet, sometimes dark purple or reddish brown, the color being due to the presence of a red pigment (*phycoerythrin*) that may be separated from the green (which may or may not be chlorophyll). In addition to the presence of phycoerythrin, one of the chief peculiarities of the group is the absence of any ciliated cells, either swimming spores or gametes, which is a surprising feature in so extensive an aquatic group. Another conspicuous peculiarity is the method of sexual reproduction, which often results in a very complicated life history.

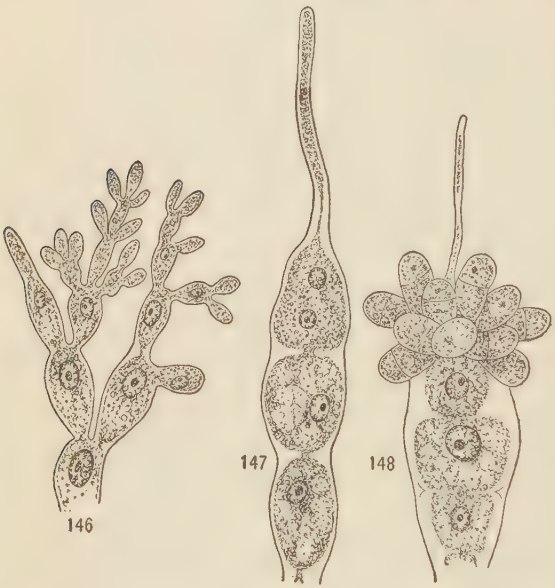
The Rhodophyceae seem to form an independent group, with no evident connections, and are certainly the most specialized of algae. The Florideae so nearly include all of the red algae that the name is often used as synonymous with Rhodophyceae. It is impossible to present adequately the maze of forms, and three of the best known are selected as illustrations, two representing the simpler forms and simpler sexual reproduction, the third representing the more complex forms and complex sexual reproduction.

Before presenting these types, mention may be made of a small group that combines certain characters of brown and red algae.

Dictyotales. — This is a small group of marine forms, of uncertain affinities, but interesting on account of the combination of characters. They are sometimes included among the brown algae, and sometimes among the red algae, so that they may well be mentioned between these two groups. The body is a narrow, repeatedly dichotomous thallus, whose pigment contains a brown constituent suggesting that characteristic of the brown algae. Sporangia are developed on the surface of the thallus, and each sporangium produces four non-motile spores (*tetraspores*), a conspicuous character of the red algae. The antheridia occur in clusters on the surface of the thallus, and produce sperms with a single terminal spiral cilium, a character that belongs neither to brown algae nor to red algae. The oogonia also are clusters of superficial cells, each one discharging a single egg, a character suggesting the egg-discharging habit of *Fucus*. In such a case, the comparative value of characters must be estimated, and perhaps tetraspore formation is to be regarded as the most important among those given. If this be true, the Dictyotales are to be considered as an aberrant group of red algae.

Nemalion. — This marine form will serve to illustrate the simpler red algae. It is a branching filament, and probably produces no tetraspores.

Antheridia. — The antheridia occur in clusters at the ends of short branches (fig. 146), each antheridium being a single cell, which at first contains a single nucleus. This nucleus divides, so that the protoplast of the mature antheridium contains two male nuclei. Physiologically, therefore, the antheridium contains two sperms, but they are not organized as morphologically distinct sperms. This binucleate protoplast is discharged from the antheridium, and not being ciliate it is carried by water currents to the female organ. This non-motile sperm, or sperm complex, is usually called a *spermatium*, but there is no special advantage in multiplying the names of a male cell. The special name was felt to be necessary when motile sperms were called *spermatozoids* or *antherozoids*, but the general term *sperm* can be applied to non-motile as well as to motile male cells.



FIGS. 146–148. — *Nemalion:* 146, branch showing antheridia forming at the tips; 147, the procarp, consisting of trichogyne and carpogonium (in the latter the male and female nuclei are observed, the former having passed in from the trichogyne); also showing two other cells with the broad cytoplasmic connections; 148, a cystocarp, showing the carpospores being cut off at the tips of short branches, which have arisen from the fertilized carpogonium.

Female sex organ. — The female sex organ of *Nemalion* illustrates, perhaps in its simplest form, this remarkable structure among the red algae, which usually consists of several cells and is called the *procarp*. In *Nemalion* the procarp consists of what may be regarded as two cells

at the end of a branch; the *carpogonium*, a cell which is the equivalent of the oogonium of other algae in that it contains the female nucleus, although no definite egg is organized; and the *trichogyne*, an elongated, hairlike cell terminating the carpogonium, which acts as the receptive cell with which the sperms come in contact (fig. 147). At first the trichogyne contains its own nucleus, but soon this nucleus disappears, and the two cells appear as a single one, with a bulbous base and a hairlike extension.

In fertilization the floating sperm comes in contact with the trichogyne, the two walls in contact become resorbed, and through the perforation one or both of the male nuclei are discharged. More than one sperm may come in contact with the trichogyne, and several male nuclei may be discharged into it; but only one passes on into the carpogonium and fuses with the female nucleus (fig. 147).

Cystocarp. — As a result of this act of fertilization, numerous short filaments are developed by the carpogonium, and at the tip of each one a spore is formed (rounded off), called the *carpospore* (fig. 148). This whole structure — carpospores, filaments, and central carpogonium — is the *cystocarp*, but it is not a cystocarp representative of this organ among the red algae, as will be seen in the other illustrations. The carpospores upon germination give rise to the sexual plants, thus completing the life history.

In such a life history, the sexual plants may be multiplied directly by tetraspores (when they occur); but the sexual act results in the formation of a cystocarp, a structure producing carpospores, which in turn reproduce the sexual plants.

Batrachospermum. — This fresh-water form is related to *Nemalion*, and will serve to illustrate other features of the simpler red algae. The life history is very much like that of *Nemalion;* but, in some cases, while the carpospores are forming, loose filaments appear as outgrowths from cells at the base of the carpogonium, representing the case of the true cystocarp of other groups, the envelope or case having suggested the name. This encasing outgrowth from adjacent sterile cells is a very common accompaniment of the act of fertilization, not only among the red algae, but also in other groups. It will be remembered that a similar envelope is developed by *Coleochaete* and by the Charales, but in the latter case it appears before fertilization.

Germination. — When the carpospore of *Batrachospermum* germinates, it gives rise to a filamentous body very different from that of the sex-

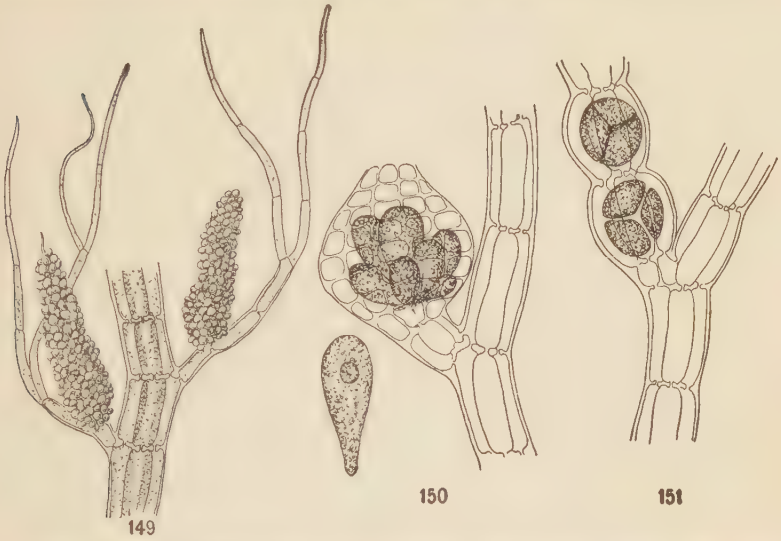
ual *Batrachospermum*, and once believed to be an independent plant it was named *Chantransia*. These *chantransia* forms multiply by spores (not tetraspores); but sooner or later one of the lateral branches develops as the sexual *Batrachospermum* filament. The *chantransia* form, therefore, is only one phase in the life history of *Batrachospermum*, giving rise to sexual branches of very different kind, which once were thought to be independent plants. It should be noted that both these phases constitute one vegetative body, the product of the carpospore. This striking variation in form, where one structure gives rise directly to a very different structure, is found in the life history of many plants, and it has been referred to in connection with the life history of Charales.

Polysiphonia. —This form is selected to illustrate the more complex and the more numerous red algae. This more complex majority includes in the life history the formation of the characteristic tetraspores, which are non-motile, naked, asexual spores, a group of four being produced by each one-celled sporangium. In the maturing sporangium there are two successive nuclear divisions, and in connection with these four nuclei the spores are organized. This definiteness in the number of nuclear divisions indicates some definite process, which will be considered later. The sporangia of red algae occur in various situations, either at the tips of short lateral branches or embedded in the thallus, in the latter case being either scattered or in special receptacles.

Polysiphonia has received its name because the complex branching filament is polysiphonous (figs. 149–151), consisting of a central row of elongated cells (axial siphon), surrounded by peripheral cells (cortical cells). Ordinarily there are three kinds of individuals: (1) male plants, bearing antheridia; (2) female plants, bearing procarps; and (3) sexless plants, bearing sporangia that produce tetraspores.

Male plant. —The antheridia occur in clusters on special branches (fig. 149). The structure of an antheridial branch is as follows: From the cells of the axial siphon large numbers of small cells arise laterally, each of which gives rise in turn to a terminal cell. An oblique division of this terminal cell cuts off a cell which is the antheridium (fig. 152). The antheridium does not discharge its protoplast as a sperm, as in *Nemalion*, but is cast off bodily, in this case the so-called "spermatium" being an antheridium that functions directly as a sperm. Its nucleus does not divide, as in *Nemalion*, so that the antheridium contains only one male nucleus. A second or even a third antheridium may be cut off successively by the same parent cell.

Female plant. — In *Polysiphonia* the procarp includes several cells in addition to the carpogonium and trichogyne. The carpogonium arises from a large cell of the axis, called the *pericentral cell*, and around



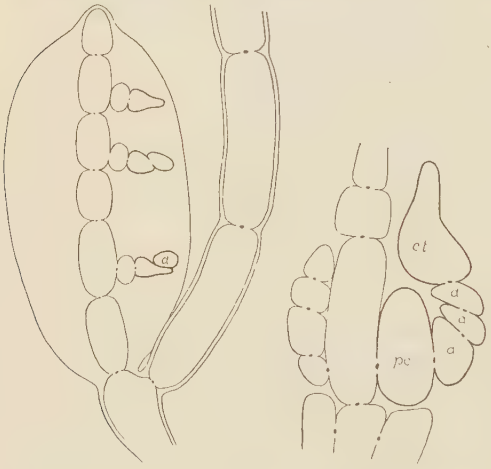
FIGS. 149–151. — *Polysiphonia:* 149, showing the polysiphonous bodies bearing two clusters of antheridia; 150, cystocarp, showing the sterile jacket investing the group of carpospores, and also an isolated carpospore; 151, two mother cells forming tetraspores.

this cell a group of *auxiliary cells* is formed, one of which crowds between the pericentral cell and the carpogonium. This whole complex structure — trichogyne, carpogonium, pericentral cell, and auxiliary cells — is the procarp (fig. 153).

Fertilization occurs as in *Nemalion*, the floating sperm (antheridium) coming in contact with the trichogyne and discharging into it its contents. The male nucleus passes to the carpogonium and there fuses with the female nucleus. The fusion nucleus divides within the carpogonium, and then what are called cell fusions begin. A passageway is opened from the carpogonium, through the intervening auxiliary cell, and into the pericentral cell, and by this means the two daughter nuclei of the fusion nucleus are free to migrate into the pericentral cell. At the same time, the auxiliary cells begin to fuse with one another and with the pericentral cell, until a large, irregular, multinucleate cell or chamber is formed. In this irregular chamber the two nuclei from the carpogonium begin a series of successive divisions, which result in a large number of

nuclei that have descended from the fusion nucleus. The irregular fusion chamber puts out lobes, into each one of which a nucleus passes and divides. At the tip of each lobe a spore is developed by a sort of budding, and into it one of the two lobe nuclei passes. In this way sixty or more carpospores are formed in a single cystocarp. The usual envelope of sterile cells, in this case an urn-shaped envelope, is developed about the whole carpospore-bearing structure from the adjacent cells (fig. 150).

Tetrasporic plant. — Upon germination the carpospores give rise to plants that produce tetraspores, but no sex organs. The sporangia arise laterally from the axial siphon, each sporangium standing on a stalk cell and finally pushing through the covering of cortical cells (fig. 151). Upon germination the tetraspores give rise to plants that bear sex organs (antheridia and procarps).



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FIGS. 152, 153. — *Polysiphonia:* 152, diagram showing formation of antheridia (*a*); 153, diagram showing structure of young procarp (*pc*, pericentral; *ct*, carpogonium and trichogyne; *a*, cells producing the auxiliary cells, one of which crowds in between the carpogonium and the pericentral). — After YAMANOUCHI.

Alternation of generations. — This remarkable life history introduces us to the alternation of generations, a type of life history that is invariable in the great plant groups above thallophytes. It is an alternation of sexual and sexless individuals, each producing spores that give rise to the other. The cytological test of alternation, referred to under *Coleochaete*, has been applied to *Polysiphonia*, and the fact of a real alternation has thus been established. It will be remembered that in such an alternation the number of chromosomes characteristic of the nuclei is doubled by the act of fertilization; therefore, the nuclei of the sexless individuals (sporophytes), which are products of fertilization, contain the double number ($2x$) of chromosomes; while the nuclei of the sexual

individuals (gametophytes) contain the half number (x). This means that in passing from sporophyte to gametophyte, $2x$ must be reduced to x. In *Polysiphonia*, the sexual individuals (gametophytes) show twenty chromosomes in their nuclear divisions, and of course this number characterizes the male and female nuclei which they produce. At fertilization the fusion nucleus receives forty chromosomes, and this number persists through the cystocarp, the carpospores, and the tetrasporic plants. This indicates that the tetrasporic plants are true sporophytes, and it is in the sporangium, in the nuclear divisions concerned in the formation of the tetraspores, that the reduction in the number of chromosomes occurs. These nuclear divisions are called *reduction divisions*, and they represent one of the two important epochs in the life history, the other being the act of fertilization. On account of the reduction division, each tetraspore contains the half number of chromosomes, and this number is continued through the sexual plant which it produces. In *Polysiphonia*, therefore, the male and female plants are gametophytes, and the tetrasporic plant is a sporophyte, the cystocarp also being sporophytic in the series of nuclei that extends from fusion nucleus to carpospore.

4. FUNGI

General character. — This enormous assemblage of thallophytes is characterized by the absence of chlorophyll, resulting in a lack of power to manufacture carbohydrate food. As a consequence, they are either *parasites*, dependent upon living plants or animals as *hosts;* or *saprophytes*, dependent upon organic débris or products from plants or animals. These are not terms of classification, for some fungi are able to live either as parasites or as saprophytes, and such are called *facultative* forms; while those restricted to either the parasitic or the saprophytic habit are *obligate* forms. The possible range of parasitism is quite different in different forms, some parasites attacking miscellaneous hosts, others being restricted to closely related hosts, others to a single kind of host, and still others attacking only certain organs (see p. 381).

The vegetative body of a fungus is the *mycelium*, composed of interwoven filaments called *hyphae*. The mycelium may be very open and delicate, or it may be feltlike, or even form a compact body (as in lichens). The mycelium establishes absorbing connections with its food supply (the *substratum*), and when these connections are definite and more or less specialized, they are called *haustoria* (suckers). In the

case of a parasite, the substratum is either the surface or the internal tissues of the host (internal or external parasites), and in such cases the haustoria are very distinct structures (figs. 1079, 1080).

Under appropriate conditions the mycelium also produces vertical branches (*sporophores*), which in a variety of ways give rise to spores. In the case of internal parasites, the sporophores reach the surface of the host, the spores thus being formed in surroundings that favor dispersal. Fungi are notable for the vast number of spores produced, and in most cases their dispersal is aerial, so that mycelia are multiplied with great rapidity and over wide areas. The sexual reproduction of fungi is exceedingly varied: in some cases the sex organs are as evident as are those of algae; in other cases the sexual act is so obscure as to raise the question whether in some life histories it has not been eliminated entirely.

Usually three great groups of fungi are recognized: (1) *Phycomycetes* (algal fungi), (2) *Ascomycetes* (sac fungi), and (3) *Basidiomycetes* (basidial fungi). The Phycomycetes differ so much from the other two groups that the latter are often spoken of together as the *Eumycetes*, or true fungi, and they contain the large majority of fungi.

(1) Phycomycetes

General character. — This comparatively small group of fungi resembles the green algae in many features, a fact which has suggested the name. It is not hard to imagine that the Phycomycetes are green algae which have lost their chlorophyll and have developed the dependent habit. Such a claim cannot be made for the Eumycetes, which have so little resemblance to the algae that any connection with them is too obscure to consider. The mycelium of Phycomycetes is composed of coenocytic hyphae, suggesting a connection with Siphonales; and this connection with green algae is further emphasized by the sex organs, which are equally prominent and of the same structure. In fact, the two groups of Phycomycetes are distinguished by their sexual apparatus: (a) *Oomycetes*, which are heterogamous, and (b) *Zygomycetes*, which are isogamous.

(a) Oomycetes

General character. — These heterogamous forms are regarded as more primitive than the isogamous Zygomycetes because they are more closely related to the algae. They are mostly aquatic and produce zoospores, in these features differing from the Zygomycetes, in which the aerial

habit is established and no motile reproductive cells are produced. However, the two groups cannot be separated rigidly upon this basis, for the aquatic habit with zoospores gradually merges into the aerial habit without zoospores. If this order of succession is true, it is an interesting illustration of the derivation of isogamy from heterogamy, which would mean a line of degeneracy so far as the apparent sexual apparatus is concerned. Illustrations of Phycomycetes may be selected from three important groups.

Chytridiales. — These are regarded as the simplest of the Phycomycetes, many of them being aquatic and parasitic on algae, and others attacking seed plants. Two of the prominent genera are as follows:

Chytridium. — A species of this genus which attacks *Oedogonium* may be used as an illustration. The zoospore has one cilium, and settling upon an oogonium sends a tube through to the egg on which it feeds. The external region of the parasite grows bulbous and functions as a sporangium, discharging zoospores which attack other plants (fig. 154). When the oospore of *Oedogonium* is formed, the fungus develops within it thick-walled resting cells; and upon the germination of the oospore, these resting cells put out tubes that produce terminal sporangia, and the infection of the oogonia of *Oedogonium* begins again. These resting cells of *Chytridium* are very commonly seen in the sexually formed spores of *Oedogonium*, *Spirogyra*, *Cladophora*, etc. In some species of *Chytridium* these resting cells are said to be formed sexually; and in another genus of Chytridiales there are antheridia and oogonia, which fuse and form the resting cell, which in that case is an oospore.

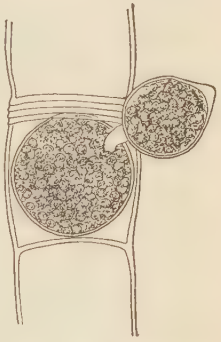


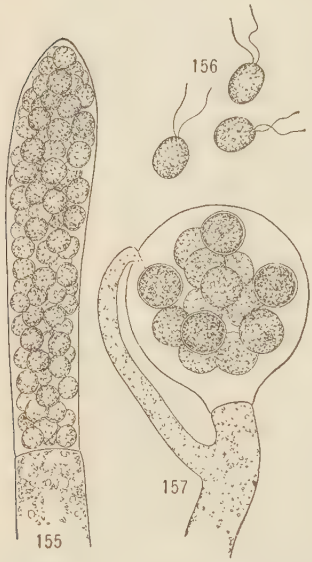
FIG. 154. — *Chytridium:* attacking the oogonium of *Oedogonium*. — After CAMPBELL.

Synchytrium. — This parasite attacks the epidermal cells of many seed plants, the uniciliate zoospores moving over the surface of young epidermis and entering the cells. In the young epidermal cell the zoospore grows as a naked protoplast, inciting the host cell to an unusual growth until it forms a blister-like pustule, distorting the adjacent tissue. Finally the protoplast develops a wall and becomes a resting cell, which in the next season sends out a swarm of zoospores. No gametes are known.

Saprolegniales. — The water molds are the most important family (*Saprolegniaceae*) of the group, being aquatics whose body resembles a

colorless *Vaucheria*. The representative genus *Saprolegnia* contains saprophytic species found on dead bodies of crustaceans, water insects, etc., and also parasitic species attacking fishes, frogs, etc. One species that attacks the eggs and young of fishes is very destructive in hatcheries.

The asexual reproduction resembles that of *Cladophora*, sporangia developing as terminal cells and producing vast numbers of biciliate zoospores, which escape through a terminal pore (figs. 155, 156). The oogonium is a spherical cell, borne terminally or laterally, and contains one to several eggs. The antheridium is tubular in form, arising from another hypha or from the same one, and grows up in contact with the oogonium in various ways, sometimes curving about it. A small fertilizing tube sent out by the antheridium pierces the wall of the oogonium, reaches an egg, and through it the contents of the antheridium are discharged (fig. 157). Fertilization results in heavy-walled oospores, which upon germination form new hyphae directly.



FIGS. 155–157. — *Saprolegnia*: 155, terminal cell producing zoospores; 156, free zoospores; 157, fertilization, showing oogonium containing several eggs, and antheridial tube piercing the oogonial wall.

Parthenogenesis. — *Saprolegnia* is notable for the frequent and perhaps usual occurrence of parthenogenesis. All stages of abortion of the male apparatus have been observed: as, for example, the antheridial tube reaching the egg but remaining closed; the tube piercing the wall of the oogonium but not reaching the egg; the suppression of an antheridial tube; or even the suppression of the antheridium. In all these cases the eggs develop as if fertilized, and produce new plants.

Experiments. — The culture of *Saprolegnia* under experimental control has succeeded in determining the conditions that favor vegetative activity, zoospore formation, and gamete formation. If well nourished, the plant vegetates indefinitely; if it is starved, as by removal to pure water, zoospore formation is induced; if the temperature is lowered, or if the plant is transferred to a solid substratum, conditions forbidding swarm spores, oogonia are formed.

Monoblepharis. — This is a form similar to *Saprolegnia* in many respects, being an aquatic saprophyte on decaying plants; but it is chiefly interesting as the only

fungus that has retained swimming sperms. These sperms are uniciliate, as are the zoospores, a fact which suggested the generic name.

Peronosporales. — These are the downy mildews, and they include many destructive parasites that live within the tissues of the host, the hyphae branching through the intercellular spaces, crowding between the cells, and sending haustoria into them. This internal mycelium sends sporophores to the surface of the host, and spores are formed by rounding off the tips of the sporophores or their branches. This process of cutting off spores is called *abstriction*, and such spores are called *conidia*. Oogonia and antheridia are formed upon the internal mycelium, and fertilization is effected through a fertilizing tube.

This is the one group of Oomycetes with distinctly aerial habit, as in the Zygomycetes; but the forms are heterogamous, and in the life history of many of them zoospores appear. The prominent genera are as follows:

Albugo. — *A. candida* is the white rust which attacks members of the mustard family, causing distortions, especially in the flower clusters. The mycelium traverses the intercellular spaces of the host, the haustoria sent into the host cells being slender branches which enlarge at the ends into little knobs. The sporophores arise in clusters and press up the epidermis, which then appears like a white blister (fig. 158). Finally the epidermis is broken and the sporophores are exposed, each ending in a chain of spores (conidia), which have been formed by successive abstrictions of the sporophore. The conidia are multinucleate, and

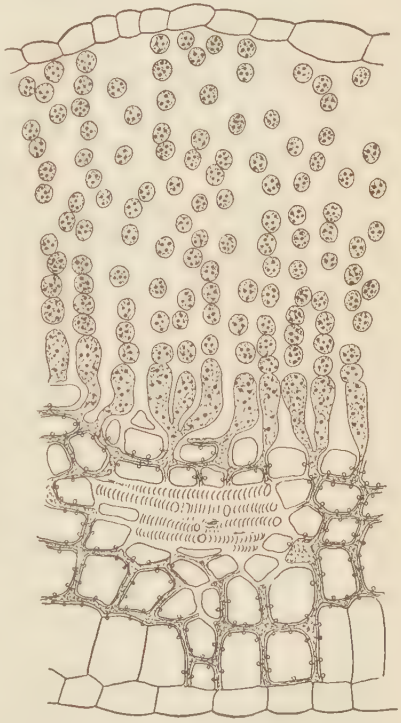


FIG. 158. — *Albugo candida* (white rust): showing mycelium crowding among host cells and sending into them small button-like haustoria, sporophores arising under epidermis and abstricting multinucleate conidia (spores), and the detached and dying epidermis. — After CHAMBERLAIN.

upon germination produce numerous laterally biciliate zoospores. The zoospores germinate promptly, each one sending out a tube that penetrates the seedling host and starts a new internal mycelium.

The sex organs of this genus are formed on the deep mycelium, the oogonia and antheridia appearing on separate hyphae. The oogonium is a globular, multinucleate cell. In the organization of the egg, the protoplast is differentiated into a peripheral zone of cytoplasm (*periplasm*), which contains all the nuclei except one, and a central mass of cytoplasm (*ooplasm*) containing a solitary nucleus for fertilization (fig. 159). The antheridium is also a multinucleate cell (fig. 160), which sends out a fertilizing tube that reaches the egg, and through this the male nuclei are discharged. One male nucleus fuses with the solitary nucleus of the ooplasm, and a heavy-walled oospore is formed. The oospore is liberated by the decay of the surrounding host tissue, and on germination either produces zoospores or develops a mycelium directly.

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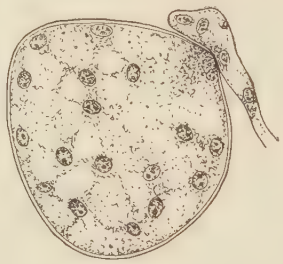

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FIGS. 159, 160. — *Albugo:* 159, oogonium showing differentiation of protoplast into periplasm (containing numerous nuclei) and ooplasm (containing one nucleus); 160, oogonium showing no such differentiation of protoplast, resulting in multinucleate fusion during fertilization; also the multinucleate antheridium in contact.

In certain other species (*A. Bliti* and *A. Portulacae*), the numerous nuclei of the egg remain distributed throughout its mass (fig. 160), and when the male nuclei are discharged, there is multinucleate fusion, many nuclei pairing and fusing.

Phytophthora. — *P. infestans* is the fungus producing potato rot, a disease of great economic importance. The mycelium vegetates in the green parts of the plant, causing wilting and withering of leaves and stem. The sporophores are sent to the surface in immense numbers through stomata, and branch, bearing solitary conidia on the branches. Damp, windy weather is said to spread the disease like wildfire. The mycelium winters in the tubers.

Plasmopara. — *P. viticola* is the grape mildew, the groups of branching sporophores appearing like downy spots upon the surface of the host (conspicuous on the leaves.) The conidia upon germination produce laterally biciliate zoospores,

as in *Albugo*, a feature which distinguishes the genus from *Peronospora*, under which the grape mildew was placed formerly. This disease is of American origin and was unknown in Europe until American grape stocks were introduced as a protection against the destructive phylloxera.

Peronospora. — These forms are very common parasites on ordinary vegetables, as peas, beans, spinach, etc., and differ from *Plasmopara* in the fact that the conidia upon germination develop a mycelium directly. In the life history of *Peronospora*, therefore, zoospores, characteristic of the Oomycetes, have been eliminated.

(b) Zygomycetes

General character. — This group of Phycomycetes is distinguished from the Oomycetes in general by the establishment of the aerial habit; by the elimination of zoospores; by so-called isogamy, so far as the sexual reproduction is known; and perhaps by the sexual differentiation of individuals, although there is no distinct development of gametes.

Mucorales. — These are the black molds, which are mostly saprophytes. The characteristic cobwebby, fleecy-white mycelium, com-

FIG. 161. — *Mucor:* diagram showing mycelium and sporophores.

posed of large, often glistening, profusely branching hyphae, is very common on decaying material, stale bread (kept moist and warm), fruits and fruit juices, etc. The ordinary form on dung is *Mucor Mucedo*, while the common bread mold is *Rhizopus nigricans* (fig. 161).

Sporangia. — The stout sporophores bear globular sporangia, the spores and stalk being dark or even black, suggesting the name black mold. After the terminal sporangium cell is cut off, the separating wall bulges into the sporangium cavity, forming the so-called *columella* (fig. 162). The sporangium wall finally becomes mucilaginous and the spores are set free and dispersed, forming new mycelia directly.

Sexual reproduction. — Sexual reproduction occurs under special conditions, when suitable individuals are brought together. The two kinds of individuals are called *strains*, and have been distinguished as (+) and (−) strains, which apparently correspond to female and male individuals. In general, the two strains are not recognizable by sight, but are known to be sexually different by their behavior. Fertile branches (*suspensors*) are developed by pairing individuals, come into contact (fig. 163), and a terminal cell (gametangium) is cut off by each (fig. 164). These two abutting gametangia are multinucleate, a perforation is developed at the contact, and the two protoplasts fuse, a very large and heavy-walled zygospore being formed (figs. 165, 166), from which a new mycelium is developed (fig. 167). In many cases the pairing suspensors and gametangia differ decidedly in size, in which case a differentiation into male and female individuals becomes visible (figs. 164–166). It has also been observed that the larger gametangia and suspensors arise from more robust mycelia, and these in turn from larger sporangia than do the smaller gametangia and suspensors. It seems possible to arrange a series of pairing gametangia, ranging from such inequality in size that the pair may be regarded as an oogonium and an antheridium (as in *Albugo*), to absolute equality. Such a series suggests a line of degenerating sexual organs, in which distinct heterogamy passes into isogamy; but of course it might be read in the opposite direction.

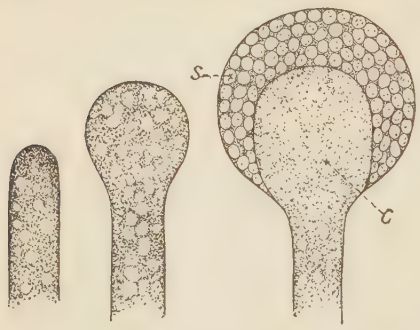
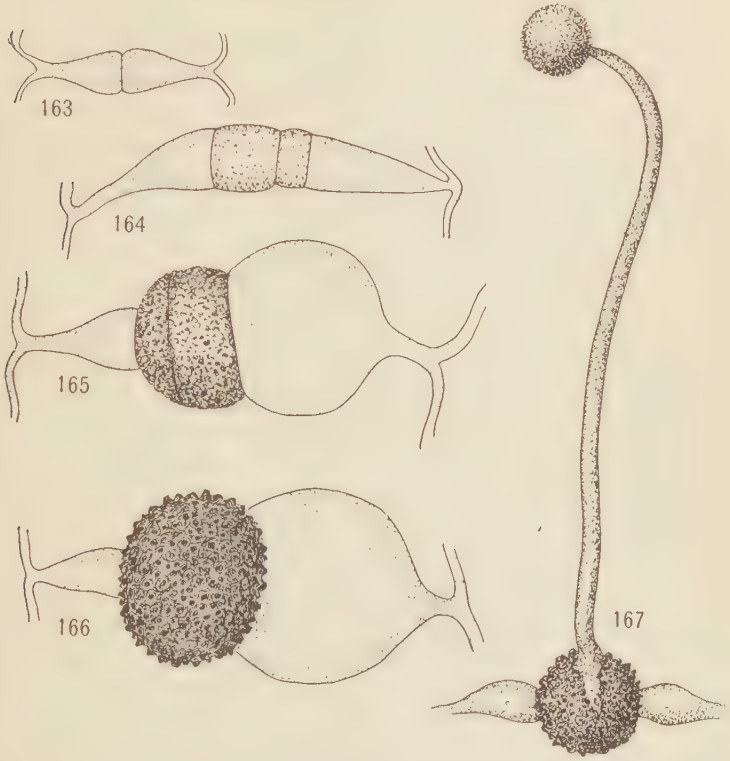


FIG. 162. — *Mucor:* showing the development of a sporangium at the end of a sporophore; in the last member of the series the spores (*s*) and columella (*c*) are evident.

Pilobolus. — This mold is abundant on stable manure, and resembles *Mucor*, but it is remarkable for the method of dehiscence of its sporangium. The sporophore becomes very turgid and swollen just beneath the sporangium and finally bursts, hurling the sporangium with considerable force. This curious habit has given to the plant the name squirting fungus. If a bell jar is placed over the plants, the inner surface becomes dotted with discharged sporangia.

Entomophthorales. — These are parasites fatal to insects, the common house fly often being destroyed by them. The spore (conidium) in germination sends

out a tube that penetrates between the body segments or through the chitinous skin of the insect. The mycelium finally kills it, filling the body in its vegetative growth. At this stage reproduction begins, the mycelium sending out numerous short branches, from which eventually sporophores arise, reaching the surface of the body and each abstricting a single conidium, which is squirted off much as is the sporangium in *Pilobolus*, the dead body of a fly adhering to a window pane often being surrounded by a "halo of spores."



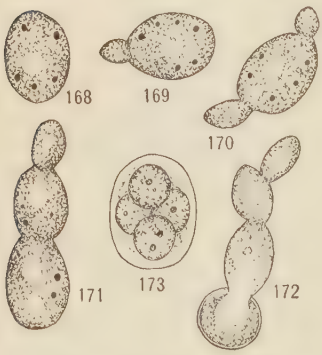
FIGS. 163–167. — *Mucor:* 163, fertile branches (suspensors) in contact; 164, gametangia (unequal) cut off; 165, 166, formation of zygospore by two very unequal suspensors; 167, zygospore producing a mycelium, which has already produced a sporangium (after BREFELD).

Conclusions. — The Phycomycetes strongly suggest relationship with the green algae, their coenocytic bodies resembling those of the Siphonales. They also show a transition from an aquatic (Oomycetes) to an aerial (Zygomycetes) habit, accompanied by a transition from zoospores to aerial spores. There is also an apparent reduction of the

sexual apparatus, from heterogamous alga-like forms to isogamous forms. At the same time, although the sex organs lose their dissimilarity in appearance, there is retained, at least in some forms, a physiological differentiation which extends to individual mycelia.

(2) Ascomycetes

General character. — The sac fungi include the majority of fungi, and their connection with the algae is very vague. In contrast with the Phycomycetes, the mycelium is composed of septate filaments, and the sex organs are much reduced and even suppressed. The common character of this great assemblage of forms is the appearance of an *ascus* (sac) in the life history, in which the *ascospores* are formed. The ascus is a special cell, usually club-shaped or elongated, which at first contains two nuclei. These nuclei fuse, and the fusion nucleus begins a series of three successive divisions, resulting in eight nuclei. About each nucleus a wall is formed, cutting out some cytoplasm, producing eight ascospores (fig. 176). These definitely three successive nuclear divisions, resulting always in eight ascospores, are found to be reduction divisions, resulting in reducing the number of chromosomes, and therefore the ascus holds the same important place in the life history of an ascomycete as does a spore mother cell in the higher plants (see p. 95). In the majority of forms, a spore case is developed in connection with the asci, more or less investing them with a protective jacket. This investing structure is the *ascocarp*, and it holds the same relation to the asci as does the cystocarp of red algae to the carpospores.



Figs. 168–173. — *Yeast:* 168, yeast cell; 169, 170, cells budding; 171, 172, sprout chains; 173, cell containing four spores. — 168–171, after Coulter; 173, after Rees.

The group is so extensive and varied that no representative forms can be selected. A few illustrations from the eight usually recognized orders are as follows:

(a) Protoascales

The yeasts (*Saccharomycetes*) are the most familiar forms, but their position here is very doubtful, for it is felt that their whole life history is probably not known. They are solitary, oval cells,

which reproduce by rapid budding, forming *sprout chains* (figs. 168–172). When cultivated under certain conditions, four internal spores are formed, and this is the only ascomycete connection (fig. 173). If the connection is a true one, the yeast cell under certain conditions becomes an ascus. The great economic importance of the group in alcoholic fermentation is well known (see Part II, p. 409).

The group Protoascales, however, is based upon a few forms with a true mycelium, which are otherwise about as simple as yeasts.

(b) Protodiscales

This is a small group parasitic on seed plants, especially trees. A characteristic genus is *Exoascus*, *E. deformans* causing the disease known as peach curl, which results in a characteristic crinkling and deformity of the leaf. The mycelium sends to the surface patches of asci, each ascus discharging eight ascospores. The form is simple in the absence of ascocarp formation, the layer of asci, called the *hymenium* or *hymenial layer*, arising from the mycelium with no accompanying sterile structure. *E. pruni* forms the so-called plum pockets, in which the young fruit becomes of abnormal size and shrivels, the asci appearing in the wrinkles. Other species of *Exoascus* form brushlike deformities on certain trees, as wild cherry, hornbeam, etc., known as witch brooms. The best-known witch brooms, however, are formed by a very different group of fungi.

(c) Helvellales

The mycelium of these forms is usually subterranean, being saprophytic on decaying organic matter, and is common in the humous soil of forests. The ascocarp is a remarkable fleshy structure, rising above the surface like a mushroom, the hymenium occurring as a superficial layer variously distributed. The best-known form is the edible morel (*Morchella*), the surface of the cap region of the ascocarp being reticulated with irregular pitlike depressions lined with hymenium (fig. 174). A section shows that the hymenium is a mixture of paraphyses (sterile filaments) and asci.

FIG. 174. — *Morchella* (morel): the fleshy ascocarp arising from the mycelium.

(d) Pezizales

General character. — The cup fungi form a very large group of saprophytes, characterized by a broadly open ascocarp lined with the hymenium. The ascocarp may take the form of a flat disk, a bowl, a cup, a funnel, and is usually called an *apothecium*, to distinguish it from

other forms of ascocarp. The group is also often called the *Discomycetes*, on account of this characteristic apothecium. In some of the forms sex organs have been discovered, and the ascocarp follows from the sexual act; in others the ascocarp may perhaps arise vegetatively, or at least from no apparent sex organs. Some familiar forms of Pezizales are as follows:

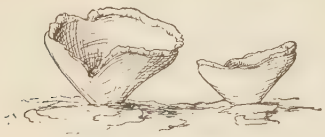


FIG. 175. — *Peziza:* ascocarps (apothecia) arising from the mycelium, and lined with the hymenium.

Peziza. — This genus is conspicuous on account of the brightly lined cups (ascocarps) that arise from the mycelium in decaying wood, humous soil, etc., one of the most common forming a cup with scarlet lining (fig. 175). In the development of the ascocarp, fertile branches (*ascogenous hyphae*) arise and give rise to asci; sterile branches intermixed with these give rise to paraphyses (fig. 176); while other investing sterile branches form the cup. The origin of these structures and their probable relation to the act of fertilization is suggested by the following investigated forms:

FIG. 176. — *Peziza:* fragment of a section through the hymenium, showing three asci, each containing eight ascospores, and the hair-like paraphyses. — After CHAMBERLAIN.

Pyronema. — In this genus well-developed sex organs have been found (fig. 177). The female sexual apparatus superficially resembles the procarp of *Nemalion* (see p. 56) in consisting of a globular cell (oogonium) and an elongated, tubelike cell (trichogyne or conjugating tube). The antheridium is a terminal, more or less club-shaped cell which comes into contact with the tip of the conjugating tube and fuses with it. The contents of the antheridium pass into the conjugating tube, whose basal wall is then resorbed, and the antheridial material passes on into the oogonium (fig. 177). Both antheridia and oogonia are multinucleate, so that fertilization consists of multinucleate pairing (see under *Albugo*, p. 66). The fertilized oogonium is cut off from the conjugating tube again by a wall, and gives rise to branch-

ing filaments (ascogenous hyphae), whose ultimate branches form asci. This fertilized oogonium giving rise to ascogenous hyphae is usually called an *ascogonium*. From hyphae beneath the ascogonium branching filaments arise that produce the colored paraphyses, and still other sterile hyphae give rise to the ascocarp (fig. 178). Usually several ascogonia are involved in a single ascocarp.

FIG. 177. — *Pyronema:* oogonium with its conjugating tube (or trichogyne); antheridium curved around the trichogyne (hence in section the latter appears as if piercing the former); trichogyne tip fused with antheridium and receiving nuclei; nuclei collecting in oogonium. — After HARPER.

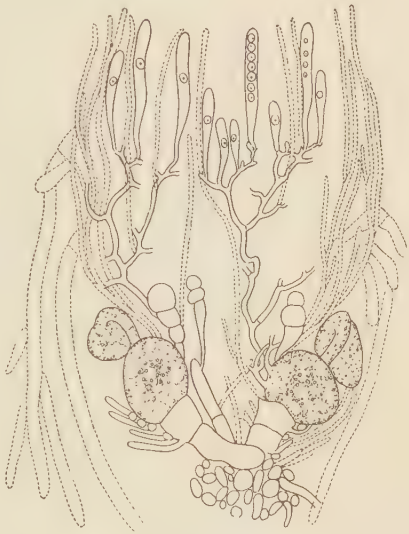


FIG. 178. — *Pyronema:* somewhat diagrammatic section of an ascocarp (involving two ascogonia), showing ascogenous hyphae arising from the fertilized oogonium (ascogonium) and producing asci. — After HARPER.

Ascobolus. — In this form structures resembling sex organs have been found, and may be interpreted with the help of the life history of *Pyronema*. From the mycelium there arises a large, bow-form, septate hypha (the "swollen hypha"), to which other slender branches become attached. No fusion has been observed, but the position of the slender branches suggests that their function may be that of antheridia. In any event, the septate swollen hypha becomes a single chamber by the disappearance of the cross walls, and then gives rise to ascogenous hyphae that bear the asci. The paraphyses and the ascocarp also arise in the way described for *Pyronema*. It seems safe to infer that the

'swollen hypha" represents the female sex organ, which by fertilization or not becomes the ascogonium.

Applying these facts to *Peziza* and to the other Pezizales, it is probable that in them an ascogonium related to a sexual act is present either actually or historically; and that the nuclear fusion, which represents the essential feature of fertilization, is likely to have persisted in the life history even though apparent sex organs may have disappeared.

(e) Tuberales

These are the truffles, whose mycelium is entirely subterranean in humous soil. A remarkable subterranean, tuber-like, fleshy ascocarp is produced, which is the edible truffle. The ascocarp completely incloses the asci, and this closed type is often designated a *cleistothecium*, to distinguish it from the open ascocarps (apothecia). The cleistothecium of Tuberales consists of a fleshy cortex and a central ascus-forming region. In maturing, the interior sterile tissue and the asci disappear, leaving the ascospores free within the cortex. Very little is known of the life history of the Tuberales. It has been suggested that the mycelium may be that of some root fungus (*mycorhiza*), for in France and Italy, the chief market sources of the truffles of commerce, they are found constantly under oak trees.

(f) Plectascales

This group comprises saprophytes with an extensive mycelium, closed ascocarps (cleistothecia) of peculiar structure, and abundant production of conidia. The best-known representatives are the blue and green molds: *Aspergillus* (*Eurotium*), the herbarium mold, also on bread, preserves, etc.; and *Penicillium*, the common blue mold on bread, etc. From the mycelia the sporophores (conidiophores) arise in profusion, and their terminal branches by abstriction produce rows of conidia (fig. 179).

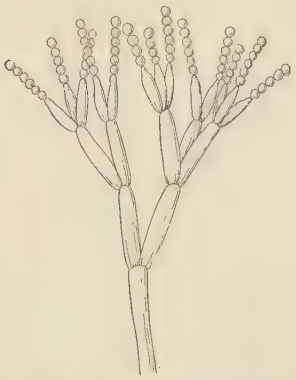


FIG. 179.—*Penicillium:* branches of a sporophore producing rows of conidia.

The sex organs are represented by two short, spirally intertwined filaments. Their fusion has not been recorded, but from one of them ascogenous hyphae arise and bear numerous small asci containing eight ascospores. At the same time, the usual investment of sterile filaments is developed and forms a compact, parenchyma-like

tissue, through which the asci are scattered. There is thus no definite layer of asci (hymenium), as in other groups, a feature that characterizes the Plectascales.

(g) Pyrenomycetales

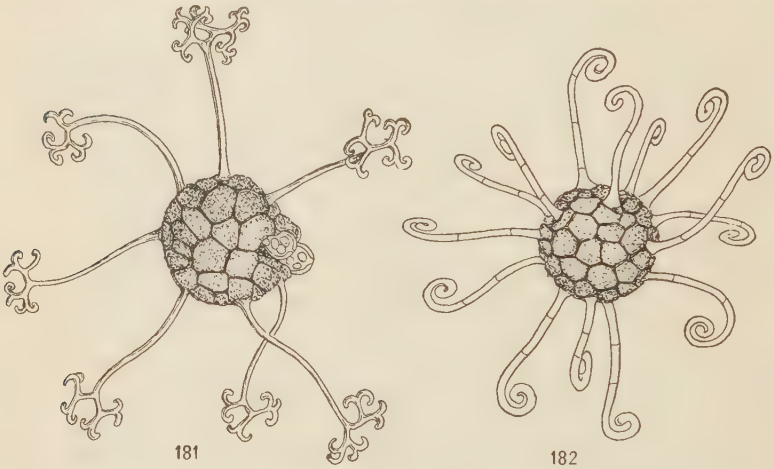
This is an enormous group of fungi, comprising thousands of species. There are two well-defined subgroups: the mildews and their allies (Perisporiales), and the black fungi (Pyrenomycetes proper). A representative or two from each subgroup will serve as illustrations.

Mildews. — These fungi form a family of Perisporiales known as the Erysiphaceae (often written Erysipheae). They are superficial parasites on the higher plants, the cobweb-like mycelium especially running over leaves, and sending out small haustoria into the epidermal cells (fig. 180). From the mycelium there arises a profusion of simple sporophores, each producing a terminal row of conidia, which multiply the parasite rapidly.

FIG. 180. — *Microsphaera* (lilac mildew): ascocarps (cleistothecia) appearing as black dots on the mycelium which spreads over the surface of the leaf.

When conidium production declines, the sex organs appear. The oogonium and antheridium are uninucleate cells at the tips of branches, develop in contact, and through the usual perforation developed in such cases the male nucleus enters the oogonium and fuses with the female nucleus. As a result of fertilization, the oogonium becomes a short filament, the ascogenous filament or ascogonium. In some of the mildews (as *Sphaerotheca*) a cell of the ascogonium becomes the solitary ascus; in others (as *Microsphaera* and *Uncinula*) one of the cells gives rise to ascogenous hyphae that produce several asci. From the cell beneath the oogonium (the stalk cell), the sterile hyphae arise that form the sheath of the closed ascocarp (cleistothecium), and from the sheath cells there arise the characteristic appendages in the form of simple hairs, dichotomously branching hairs, hairs with hooked tips, etc. (figs. 181, 182). The ascocarps appear on the mycelium as small black or brownish dots irregularly scattered (fig. 180).

Black fungi. — This (Pyrenomycetes proper) is an exceedingly large and varied group, characterized by a flask-shaped ascocarp opening at the top (*perithecium*) and lined by the hymenial layer of asci and hair-like paraphyses (fig. 184). It includes parasites on various parts of plants, especially cortex and leaves; and also saprophytes on decaying wood, etc., often forming black spots, knots, etc., resembling charred places and suggesting both the technical and common names. The perithecia arise either singly on the mycelium, appearing as small black



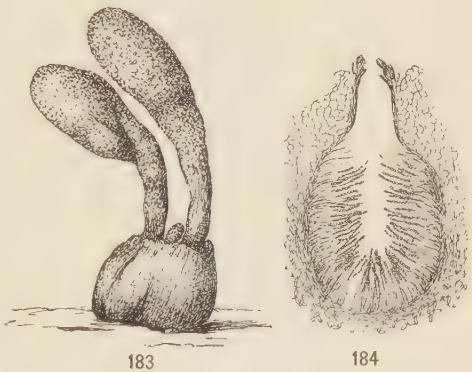
FIGS. 181, 182. — *Mildews:* 181, ascocarp of *Microsphaera*, showing the heavy case, dichotomous appendages, and asci crushed out of the case; 182, ascocarp of *Uncinula*, with hooked appendages.

dots irregularly scattered, as in the mildews; or they occur in groups embedded in a variously shaped mass of compact (parenchyma-like) mycelium, the whole structure being known as the *stroma* (pl. *stromata*). A simple illustration of each kind will be given.

Black knot (*Plowrightia morbosa*). — This is a destructive disease that attacks the plum and cherry (fig. 1100). In the spring the mycelium is under the bark; then it breaks through, beginning the knot, which may become quite large and solid, composed of the mycelium of the parasite and hypertrophied host tissue. Numerous sporophores arise from the mycelium, abstricting conidia; and in the autumn the perithecia appear over the surface of the knot as small papillae, open at the top and lined with a hymenial layer. In the following spring the ascospores escape and begin fresh infections.

Ergot fungus (*Claviceps purpurea*). — This is a common parasite on young ovaries of grasses, especially rye. The ascospores infect the ovaries in early summer, and on account of the growth of the mycelium the ovary becomes enlarged and deformed. The mycelium produces abundant sporophores, the conidia being abstricted in clusters, and also excretes copious honey dew, which is sought by insects, and in this way the embedded conidia are carried to other ovaries.

After the absorption of the tissues of the ovary, the mycelium becomes transformed into a compact, parenchyma-like mass, the *sclerotium* (fig. 1120). These elongated, dark violet, often curved sclerotia, replacing the ovaries and projecting from the spike, are the so-called *ergot*, the source of the astringent drug that bears the same name. The sclerotia fall to the ground and pass the winter. In the spring, when the rye is in flower, the sclerotia produce radiate patches of hyphae, that in turn give rise to long-stalked, rose-colored, globular heads (stromata), in which are numerous sunken perithecia which communicate with the surface through porelike openings. The ascospores are remarkable in being very long and filiform, and are carried by the wind to the flowering spikes.



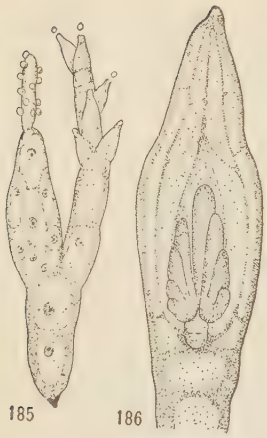
183 184

FIGS. 183, 184. — *Xylaria:* 183, club-shaped stromata arising from the sclerotium, the surface perforated by the porelike openings of the perithecia; 184, section through a perithecium, showing asci and paraphyses; the ascus wall is so delicate that the row of ascospores is the conspicuous feature.

Xylaria, which belongs here, is a very common saprophyte, forming conspicuous hard black masses on dead wood. From the sclerotium there arise club-shaped stromata (fig. 183), whose surfaces are perforated by the very numerous porelike openings of the perithecia (fig. 184).

(h) Laboulbeniales

This is a remarkable group of fungi parasitic on insects, especially aquatic forms. The sexual apparatus is much like that of the red algae, the procarp consisting of carpogonium, trichogyne, and auxiliary cells; and the antheridia producing sper-



FIGS. 185, 186. — *Stigmatomyces:* 185, sex organs; right branch showing antheridia discharging spermatia; left branch being a procarp showing trichogyne (with attached spermatia), carpogonium, and auxiliary cells; 186, the formation of asci within the perithecium after fertilization. — After THAXTER.

matia that fuse with the trichogyne (fig. 185). Perithecia are formed, and the asci bud out from the auxiliary cells (fig. 186), the whole process suggesting the formation of cystocarps among the red algae.

Lichens

General character. — With a few exceptions (p. 91), lichens are Ascomycetes parasitic upon certain algae, the relation between the two organisms being so intimate as to result in a structure resembling a single organism. The dual nature of lichens was announced by Schwendener in 1868, but it was many years before the proof of it became convincing. In 1889 Bonnier began to synthesize lichens; that is, to bring together "wild algae" and lichen fungi and thus produce artificial lichens. The parasitism is peculiar in that the algae do not seem to be harmed in most cases, the cells being rarely penetrated by the fungus. The algae concerned in lichen formation are for the most part Cyanophyceae and Protococcales. As would be expected, the algae thrive without the fungus, just as do the wild species; but the lichen fungus soon perishes if it does not come into contact with the appropriate algae. (See p. 91 and fig. 1117.)

Body. — The lichen fungus usually forms a thallus body much more definite and differentiated than do other mycelia, the thallus often resembling in form that of certain liverworts. In structure, there is a distinct compact cortical region and a central looser region, in either of which the algae may occur (fig. 190). Two structural types of thallus body are recognized, dependent upon the distribution of the algae: (1) *homoiomerous*, in which the algae are scattered; and (2) *heteromerous*, in which the algae occur in layers.

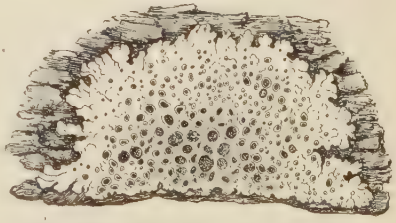


FIG. 187. — *Physcia:* a flat foliose lichen on bark, showing numerous shallow apothecia. — After COULTER.

On the basis of habit, three types are recognized: (1) crustose lichens, with an undefined mycelium often penetrating the substratum; (2) foliose lichens, with a definite liverwort-like thallus, which has marginal growth and rhizoids (as *Physcia*, fig. 187, and *Parmelia*, fig. 188); and (3) fruticose lichens, which are erect and often branching (as *Cladonia*, the reindeer moss), or pendent and branching (*Usnea*, fig. 189).

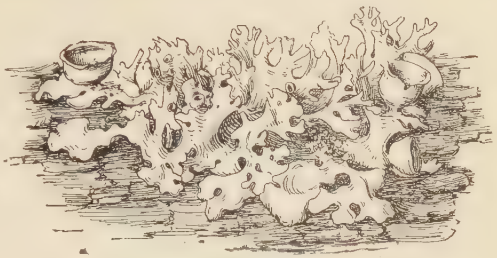


FIG. 188. — *Parmelia:* an almost free foliose lichen on bark, showing cuplike apothecia.

Vegetative multiplication is secured by *soredia*, which are scalelike or globular bodies, composed of a little tangle of mycelium with some algal cells (figs. 1114–1116). The ascocarps are very conspicuous structures, usually being apothecia (disklike forms), but some are perithecia. The hymenium is the usual mixture of asci and paraphyses, and the ascus produces the usual eight ascospores.

FIG. 189. — *Usnea:* a pendent and branching fruticose lichen, bearing conspicuously flaring apothecia.

Sex organs. — The sex organs of the lichen fungus are evident in some cases. The antheridia occur on branching hyphae within a conceptacle-like chamber called the *spermogonium*. They are very small cells that bud out and become abstricted, suggesting conidia, as they have often been considered. These antheridia are cast off and function directly as sperms, as is true of certain of the red algae, and they are also called spermatia.

The female sex organ also suggests that of the red algae. It is a multicellular filament spirally coiled and terminating in a filamentous extension to the surface of the thallus. The spirally coiled region has been called the *archicarp*, and the filamentous extension to the surface

the *trichogyne*. The spermatia have been found attached to the exposed tip of the trichogyne, with their nuclei gone; so that discharge and nuclear fusion seem to be safe inferences. The archicarp then enlarges and divides, becoming transformed into the ascogonium, from which arise the usual ascogenous hyphae. From hyphae beneath the ascogonium the sterile branches arise that produce the investing sterile tissue of the ascocarp, the whole structure finally breaking through the surface of the thallus, usually in the form of a disklike or saucer-like ascocarp (apothecium, fig. 190). One ascocarp may involve a single ascogonium or several, just as described under Pezizales (see p. 73).

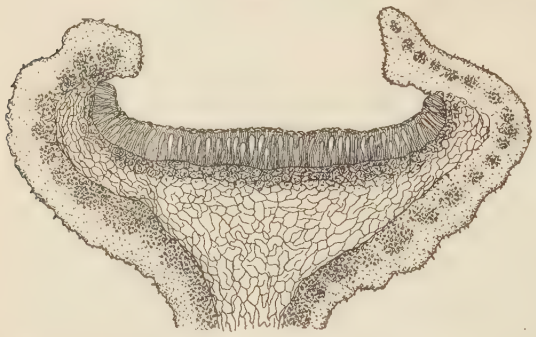


FIG. 190. — *Anaptychia:* section of an apothecium of a lichen, showing the hymenium made up of asci and paraphyses overlying the inner loose mycelium of the lichen body, and all invested by a thick cortical mycelium, within which are apparent groups of algae. — After SACHS.

(3) BASIDIOMYCETES

This great group of fungi is characterized by the occurrence of a *basidium* in the life history. A basidium is the swollen end of a hypha, and consists of four cells or one cell; but in either case it usually gives rise to four slender branches (*sterigmata*), and each sterigma cuts off at the tip a spore (*basidiospore*) (fig. 201). The basidium holds the same place in the life history of a basidiomycete that an ascus does in the life history of an ascomycete. The essential feature of a basidium is that it produces spores externally and that the theoretical number of spores is four. As in the history of the ascus, the young basidium contains two nuclei which fuse. Unlike the ascus, however, the fusion nucleus of the basidium, by two successive divisions, gives rise to four nuclei, and it is these four nuclei that are found in the four spores. In some cases four sterigmata are not produced and four spores are not formed, but four nuclei appear in the basidium.

Among the higher Basidiomycetes the basidia form a definite layer (hymenium), whose structure and position are important in classification. As yet, the classification of this great group is very uncertain, but for our purpose two great series may be recognized.

I. *Protobasidiomycetes*, in which the basidium is four-celled, each cell bearing a spore; and II. *Autobasidiomycetes*, in which the basidium is one-celled and bears four spores (or at least produces four nuclei).

I. Protobasidiomycetes

(a) Ustilaginales

General character. — These are the smuts or brand fungi, destructive parasites that attack the floral and other organs, notably the ovaries of grasses, and are of course best known in connection with their ravages among cereals. *Ustilago Maydis*, the corn smut, may be taken as a representative.

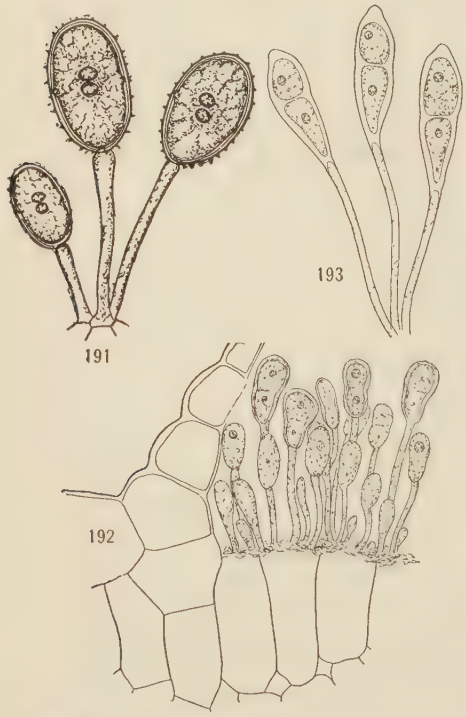
Corn smut. — The mycelium may infect any part of the host, even the roots, and may give external indications of its presence in any region. At the time of flowering, for example, the ovary may become packed with mycelium, which causes a distorted, swollen, tumor-like growth. These tumor-like swellings may be observed also in other parts of the plant, including the tassels. Later this mycelium forms additional cross walls; the short cells become rounded off and thick-walled, and the mycelium is thus transformed into a mass of black spores, which are the so-called brand spores, the whole mass being the so-called smut. This kind of heavy-walled spore, which is a transformed vegetative cell of a septate mycelium, is called a *chlamydospore*, the name referring to the heavy, protective wall. These spores fall to the ground and pass the winter. Upon germination in the spring, the spore develops a short filament of three or four cells. This filament is saprophytic and each cell buds out spores laterally and the end cell terminally, suggesting conidium-formation. If abundant food supply is available, spores continue to be abstricted in great numbers, and may be multiplied further by the yeastlike budding of the spores (see p. 70). This filament of three or four cells is thought to represent the basidium, but in this case the very indefinite number of spores produced obscures the resemblance. The spores produced, therefore, are probably basidiospores, and the brand spores hold the same place in the life history of smuts as that held by the teleutospores in the life history of rusts

(see p. 82). The basidiospore develops a mycelium that penetrates the young host plant.

(b) Uredinales

General character. — These are the well-known rusts, all of them being destructive parasites, whose mycelia live in the intercellular spaces of higher plants, especially in the leaves. The best-known form is *Puccinia graminis*, one of the wheat rusts, and an outline of its life history will serve as an illustration of the group.

Wheat rust. — The mycelium traverses the tissues of the young wheat plant, and during the growth of the host it sends to the surface numerous sporophores, each bearing a single spore, the *uredospore* (fig. 191). The groups of uredospores (summer spores) on the surface of the host form reddish spots or lines, giving rise to the name rust or red rust. By means of the uredospores the disease spreads rapidly through the growing wheat, the spores falling on the surface of uninfected wheat plants and sending out germ tubes that penetrate the host and form new mycelia. As the wheat plants mature, the mycelium sends to the surface of the host another kind of spore, the *teleutospore*, which is two-celled and thick-walled (figs. 192, 193). The teleutospores (winter spores) are the winter stage of the parasite, germinating in the following spring.



FIGS. 191–193. — *Wheat rust:* 191, uredospores (summer spores) (after COULTER); 192, group of young teleutospores (winter spores), among which there may be some uredospores (after CHAMBERLAIN); 193, mature teleutospores.

Basidium. — The germination of the teleutospore

results in a filament of four cells, each of which gives rise to a slender branch bearing a spore (fig. 194). This saprophytic filament has been called the *promycelium*, and its spores *sporidia;* but it represents a four-celled basidium bearing basidiospores, and is the structure that determines the position of rusts among Basidiomycetes.

FIG. 194. — *Wheat rust:* teleutospore producing basidia ("promycelia") bearing basidiospores ("sporidia"). — After TULASNE.

Aecidium. — The basidiospores that fall upon young barberry leaves germinate, and an extensive mycelium is developed among the tissues of the new host. This mycelium develops very evident structures of two kinds. Opening usually upon the upper surface of the leaf, small, flask-shaped organs appear, known as *spermogonia*, within which there arise slender filaments that form by successive abstrictions numerous very small cells, the *spermatia* (fig. 195). The names spermogonium and spermatium indicate the belief that this structure is the male apparatus, to be compared with a male conceptacle in *Fucus* (see p. 50). However, this function has not been demonstrated, and some regard them as spore-producing structures, in which case they are spoken of as *pycnidia* producing *pycnidiospores*. If this is a sexual apparatus, it would seem to be a vestigial one.

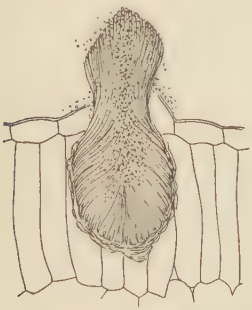


FIG. 195. — *Wheat rust:* a spermogonium (producing spermatia) arising from the mycelium of the barberry leaf. — After CHAMBERLAIN.

The other structure produced by the mycelium in the barberry leaf is the *aecidium* or *clustercup*. The aecidia usually appear in groups on the lower leaf surface, each opening upon the surface as a cup containing numerous simple sporophores bearing rows of spores, the *aecidiospores* (fig. 196). The scattered aecidiospores that fall upon young wheat plants germinate, the host is penetrated, and the mycelium is produced that begins to form uredospores.

Polymorphism. — In this life history the fungus passes through three distinct phases (the parasitic mycelium bearing uredospores and

teleutospores, the saprophytic promycelium or basidium bearing basidiospores, and the parasitic mycelium bearing aecidiospores), lives upon two unrelated hosts, and produces four (perhaps five) kinds of spores. It is natural that such a polymorphous plant should not have been understood at first, and that the different phases should have received different names. The mycelium bearing uredospores was named *Uredo;* that bearing teleutospores, not known at first to be the

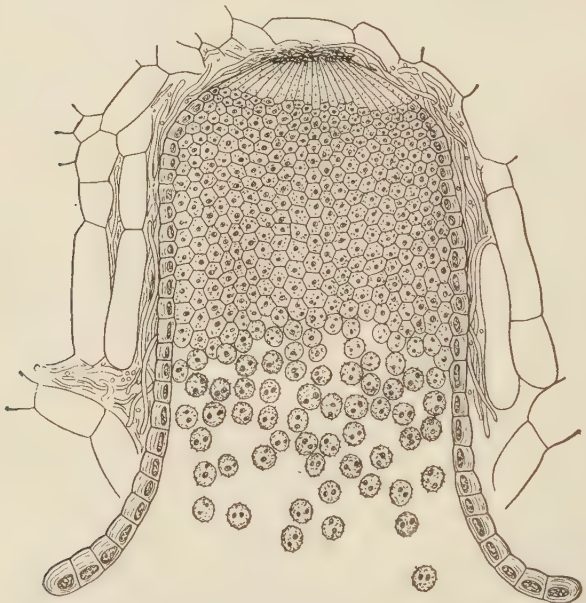


FIG. 196. — *Wheat rust:* an aecidium (clustercup) arising from the mycelium of the barberry leaf, and showing the rows of aecidiospores. — After CHAMBERLAIN.

same mycelium, was named *Puccinia;* and the form parasitic on the barberry was named *Aecidium.* Now the name *Puccinia* is retained for the plant, and the other names are used for convenience in designating the respective stages. Not all rusts include two hosts in their life history, and it is usual to distinguish rusts as *autoicous* (those having one host) and *heteroicous* (those having more than one host).

Alternation. — Recently the nuclear changes in the life history of wheat rust have been traced. In the aecidium, the cell which produces a row of aecidiospores contains two nuclei, which have been brought together in a single cell somewhere in the mycelium. In the subsequent cell divisions the two nuclei divide independently, so that each aecidiospore contains two nuclei. This binucleate condition con-

tinues in the uredospore-producing mycelium, in the uredospore, and in the young teleutospore. In the maturing teleutospore, however, the nuclei fuse, so that the cells of the mature teleutospore are uninucleate. This uninucleate condition continues in the cells of the basidium (promycelium), in the basidiospores (sporidia), and in the mycelium on the barberry. Some investigators see in this nuclear history an alternation of generations, the double number of chromosomes ($2x$) being represented by the two nuclei, and the reduction division (resulting in the x number) occurring in the formation of the four cells of the basidium. If this view is correct, the mycelium on wheat is a sporophyte, and the mycelium on barberry is a gametophyte.

Other rusts. — Owing to its infrequency in those regions, it is evident that barberry cannot be a general host in the chief wheat-producing areas of North America. Much of the rust attacking the wheat in these fields is not *P. graminis*, but one or more other species whose aecidia develop upon other intermediate hosts. It has been discovered also that uredospores may retain their vitality throughout the winter and attack directly the young wheat in the spring, thus eliminating the need of an aecidium host. It has also been claimed that the basidiospores may germinate upon very young wheat plants and infect them, but the claim is very doubtful.

The common species of wheat rust mentioned above have now been broken up into numerous species and varieties upon what are called physiological characters. This means that although they may be alike in their appearance, they can be distinguished by their behavior in the selection of hosts.

As might be expected, the complete life histories of comparatively few rusts having different hosts are known. The two hosts do not suggest one another, and therefore numerous rusts in their various stages are described as *Uredo*, *Puccinia*, and *Aecidium*, without any knowledge as to the forms that belong together in a single life history. Recently the work of linking these forms together has gone forward with considerable rapidity. The following list will serve as an illustration of a few of the results, showing also the unrelated character of hosts:

Uredo-Puccinia host	*Aecidium host*
Cereals	Barberry, buckthorn, etc.
Poa	Buttercup
Pea	Euphorbia
Senecio	Pine
Heaths	Spruce
Juniper	Apple, haw, etc.

(c) Auriculariales

These are the ear fungi, appearing as gelatinous, earlike growths on bark, board fences, etc., a very common form being seen on old stems of elder. When moist, the ear is gelatinous and brightly colored; when dry, it becomes hard and gray and wrinkled, and externally hairy. This ear is a complex sporophore arising from a mycelium, its internal surface being lined with a hymenium. A section of the hymenium shows basidia transversely divided into four cells, each cell giving rise to a slender branch (sterigma) which produces a basidiospore. This basidium so much resembles that of the Uredinales (the promycelium) that the ear fungi are sometimes grouped with them; but the complex sporophore is distinctly like that of the fleshy fungi.

(d) Tremellales

These fungi also appear as gelatinous growths on decaying wood and tree trunks, these growths being complex and more or less indefinite sporophores from a mycelium. When moist, they appear usually as thick, wavy, or folded coatings of quivering gelatinous consistency and indefinite form. The wavy ridges are coated with a hymenial layer, and the basidia are peculiar in being divided longitudinally into four cells, each cell terminating in a long, slender filament (sterigma) bearing a basidiospore.

II. Autobasidiomycetes

These are the true Basidiomycetes, the basidium being one-celled, and they constitute the large assemblage of forms known as the fleshy fungi. Two great subgroups are recognized: (I) *Hymenomycetes*, in which the hymenium is exposed; and (II) *Gasteromycetes*, in which the hymenium is inclosed.

1. *Hymenomycetes*

(e) Dacromycetales

These forms are interesting on account of their evident relationship to the Tremellales, which they resemble in their gelatinous sporophores. The one-celled basidium forks into two long sterigmata, and hence produces two basidiospores. It has been discovered that the nuclear fusion in the basidium is followed by two successive divisions, resulting in four nuclei, as in all basidia. In spore formation two nuclei remain in the basidium, or the two nuclei may move in pairs into the sterigmata, one of each pair entering the terminal spore.

(f) Exobasidiales

This group of parasites attacks, among other hosts, members of the heath family, as huckleberries, cranberries, etc., the tips of the shoots, buds, flowers, or young ovaries of the host becoming enlarged and distorted into gall-like growths. These affected parts finally become covered with a whitish bloom, made by the basidia

coming to the surface, after having broken through the epidermis. These basidia, each bearing four spores, arise directly from the mycelium, without any complex sporophore formation, differing in this respect from the following groups.

(g) Thelephorales

The sporophores of these forms appear on tree trunks as flat and tough leathery incrustations, the hymenium spreading over the smooth upper surface; or as brackets raised above the substratum, the hymenium extending over the under surface; or as funnel-shaped bodies lined with the hymenium. The general character of the sporophore distinguishes this group from the next; and the indefinite extent of the hymenium over the sporophore distinguishes both groups from those which follow.

(h) Clavariales

These are the coral fungi, with fleshy sporophores that often simulate branching coral in form, the hymenium covering the whole surface of the branches. There are also unbranched, club-shaped sporophores; but all are characteristically fleshy and hymenium-covered.

(i) Agaricales

This is by far the greatest group of fleshy fungi, containing most of the so-called mushrooms and toadstools. The complex sporophore is

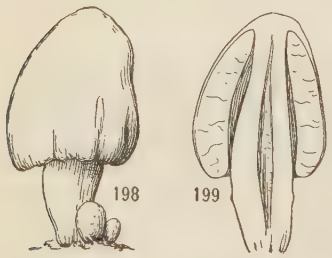
FIG. 197. — *Lepiota:* a common edible mushroom. — After COULTER.

usually definite in form, being differentiated into *stipe* and *pileus* (fig. 197), the latter having special surfaces for the hymenium. The principal families are as follows:

Hydnaceae. — These are the tooth fungi, so named because the hymenium covers toothlike or spinelike processes. In simpler forms the sporophore resembles an incrustation, in which case the teeth are on the upper surface. In other cases the teeth occur on the under surface of a bracket-like sporophore; while in *Hydnum* they are upon the under surface of the pileus of a mushroom-like sporophore.

Polyporaceae. — These are the pore fungi, so named because the hymenium lines tubes that terminate on the surface with porelike openings. The sporophores may be incrustations, with pores on the upper surface; or bracket forms (as *Polyporus*), with pores on the under surface; or mushroom-like forms (*Boletus*), with pores on the under surface of the pileus. The incrusting forms and the hard, gray, hoof-shaped bracket forms are very common on tree trunks, fallen logs, stumps, etc. Many are destructive to trees, the mycelium spreading extensively under the bark and through the wood.

Agaricaceae. — These are the gill fungi, being the common mushrooms and toadstools, and the largest family of fleshy fungi. There are bracket forms, but the prevailing type of sporophore is the mushroom, with stipe and pileus (figs. 198, 199); and in every case the hymenium covers bladelike plates, which are the *gills* (figs. 200, 201). Many of the Agaricaceae also are destructive parasites on trees, the mycelium penetrating the host extensively.



FIGS. 198, 199. — *Coprinus:* 198, habit, showing stipe and pileus, and young sporophores; 199, longitudinal section, showing relation of stipe and pileus.

The development of the characteristic sporophore is as follows. The small *buttons* consist of interwoven hyphae. Soon the rudiments of stalk and pileus appear inclosed in a loosely woven envelope (*volva*). The elongation of the stipe ruptures the volva, whose torn remnant may form a ring or sheath about the base of the stipe. In many cases a membrane (*velum*) of hyphal tissue extends in the young sporophore from the margin of the pileus to the stipe, covering the gills. When the velum is ruptured by the growth of the pileus, it may remain as a ring of tissue (*annulus*) about the stipe (fig. 197).

The presence of two nuclei in the young basidium, the nuclear fusion, the two successive divisions, the migration of the four nuclei into the four sterigmata and

so into the basidiospores, have all been observed in mushrooms. In the common field mushroom (*Agaricus campestris*) the basidium often produces only two sterigmata and spores, but in such cases four nuclei have been observed in the mature basidium. The vegetative mycelium has been observed to be binucleate, the condition found in the uredospore-teleutospore mycelium of rusts. With a uninucleate basidiospore and a binucleate mycelium, it is a matter of interest to determine where the binucleate condition originates. It is suggested that the basidiospore upon germination becomes binucleate. In that case, if the interpretation applied to the rusts (see p. 84) obtains among the mushrooms, the mycelium with its sporophore is the sporophyte, and the basidiospore represents the gametophyte.

FIG. 200. — *Coprinus:* section of under side of pileus, showing section of the stipe in the center, and the radiating (sometimes branching) gills coated by the hymenium.

2. *Gasteromycetes*

These are the most highly organized of the fungi, the complexity appearing in the structure of the sporophore. The hymenium is inclosed within the sporophore, which opens only after the spores are mature. The sporophore is differentiated into an outer zone of cortical hyphae (*peridium*) and an inner mass of tissue (*gleba*) which contains the numerous basidium-bearing chambers. These chambers either are filled with loosely woven hyphae whose lateral branches terminate in basidia, or are lined by a definite hymenial layer. The gradually increasing complexity of the sporophore will be observed in the following groups:

FIG. 201. — *Coprinus:* section of the hymenium, showing basidia bearing basidiospores; the curving of the basidia makes it impossible to show their actual connections in a section.

(j) Hymenogastrales

This group contains the simplest Gasteromycetes, and the name suggests characters belonging to both Hymenomycetes and Gasteromycetes. The peridium is simple; that is, it does not develop in layers, and ruptures irregularly. The gleba is not chambered, the basidia simply terminating lateral branches of the glebal hyphae.

(k) Sclerodermales

In this group the nearly spherical sporophores have a thick leathery (light brown) peridium, which finally becomes cracked or ruptured at apex. The leathery peridium suggested the name of the group. The gleba is chambered, but the chambers are filled with interwoven hyphae whose lateral branches bear pear-shaped basidia, upon which appear four sessile spores, sterigmata not being formed.

(l) Lycoperdales

These are the true puffballs, with globular sporophores which sometimes reach 50 cm. in diameter. The peridium is distinctly two-layered and with definite dehiscence. In *Lycoperdon* the outer layer of the peridium gradually flakes off, and the inner layer bursts at the apex. In *Geaster* (earth star) the outer layer splits into stellate spreading segments, and the inner layer dehisces by a terminal pore (figs. 1123, 1124).

The gleba contains numerous distinct chambers lined with a hymenial layer and also containing a *capillitium*, which is a fibrous structure of interwoven branching hyphae arising from the wall of the chamber and aiding in the dispersal of the spores.

(m) Nidulariales

These are the nest fungi, as the name suggests. The separate chambers of the gleba become invested each by a membrane of interwoven hyphae, and at maturity become freed by the breaking down of the intervening tissue. When the peridium opens, forming a cuplike structure, the free, membrane-covered hymenial chambers are seen lying like eggs in a nest.

(n) Phallales

These are the stink horns, whose sporophore is more complex than that of any other fungi. The sporophore develops on the mycelium as a white, egg-shaped body. The peridium is two-layered, but the tissue within, which is all gleba in the other groups, is differentiated into a central hollow cylindrical axis and an investing dome-shaped and chambered gleba. At maturity the cylindrical axis elongates with great

rapidity into a stout, hollow stalk, bursts through the peridium, and carries up on its summit the caplike and chambered gleba, the whole structure suggesting a stipe and pileus. The gleba thus exposed deliquesces into a slimy, dripping mass with the odor of carrion, which attracts carrion flies, by whose agency the embedded spores are dispersed.

Lichens

The Ascomycetes, with a few exceptions, are the lichen formers (see p. 78), and these exceptions are basidiomycetes. These lichens are the tropical *Cora pavonia*, of loose texture, whose mycelium produces basidia at the surface, instead of the ordinary ascocarp, and a few related forms.

CHAPTER II — BRYOPHYTES

Introductory. — This great division of plants comprises the liverworts (*Hepaticae*) and mosses (*Musci*). The conspicuous features of the group as contrasted with thallophytes are as follows:

1. The establishment of a definite *alternation of generations.* Distinct sexual and sexless individuals alternately produce each other, the gametophyte producing the sex organs (containing gametes), the sporophyte producing the asexual spores. The two generations are further distinguished by their chromosome numbers: the $2x$ number arises from the fusion of the sexual cells, and occurs in all the cells of the sporophyte; and the x number occurs in all the cells of the gametophyte, the reduction taking place in connection with the formation of the tetrad of spores by the mother cell.

2. The appearance of the *archegonium.* This female sex organ is very characteristic of the groups that possess it (bryophytes, pteridophytes, and gymnosperms). On this account they are often spoken of collectively as archegoniates, but the groups are too unrelated to deserve a collective name. The archegonium is a flask-shaped organ, consisting of a jacket of sterile cells (neck and venter) surrounding an axial row of cells (neck canal cells, ventral canal cell, and egg) (fig. 219). The cells of the axial row are doubtless to be regarded as potential eggs, only the innermost one maturing and functioning as an egg, the others breaking down and leaving an open canal to the egg.

3. The appearance of a *multicellular antheridium.* Multicellular sex organs and even multicellular antheridia appear among the algae, as in *Ectocarpus* (see p. 46) and Charales (see p. 42), but the antheridium of bryophytes is a very uniform and characteristic structure. It is more or less stalked, and consists of a single layer of sterile jacket cells investing a mass of small cubical sperm mother cells (fig. 210). The sperm is also of a definite kind, consisting of a small, more or less spirally curved body bearing a pair of long terminal cilia (fig. 211).

1. HEPATICAE

General character. — The liverworts are of great interest on account of their apparent relationship to the green algae on the one hand, and to the higher plants on the other. Through them the aerial habit of green plants seems to have been established. This change in habit involved more compact and better protected bodies, and the change from swimming spores to aerial spores; but it is important to note that the swimming habit was retained by the sperms. Three groups of liverworts are recognized, each having developed special features: (1) *Marchantiales*, (2) *Jungermanniales*, and (3) *Anthocerotales*.

(1) Marchantiales

This group may be represented by its two prominent families, *Ricciaceae* and *Marchantiaceae;* the former representing the more primitive forms, the latter the highly specialized forms.

Ricciaceae. — The genus *Riccia* (including *Ricciocarpus*) contains aquatic as well as terrestrial species, so that this family belongs to both the water and the land.

Gametophyte. — The gametophyte is a flat, dorsiventral body and branches dichotomously (fig. 202). This dorsiventral habit results in a differentiation of the body into two distinct regions. The dorsal (upper)

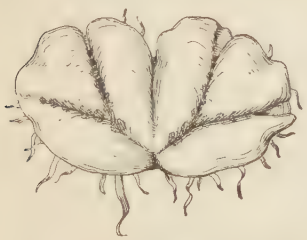


Fig. 202. — *Riccia:* showing the dorsiventral, dichotomously branching gametophyte, which puts out rhizoids and scales from its ventral surface; the rows of dark bodies in the bottom of the conspicuous grooves on the dorsal surface are sporophytes, which show also the position formerly occupied by the archegonia.

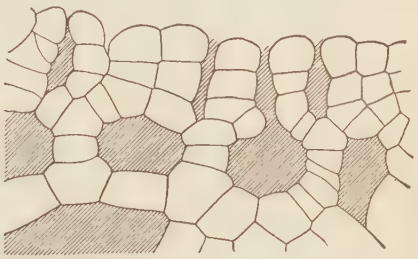


Fig. 203. — *Riccia:* section through dorsal region of thallus, showing the intercellular clefts, often enlarging into chambers, by means of which the cells containing chloroplasts are bathed by an internal atmosphere. — After Barnes and Land.

region is composed of green tissue, the intercellular spaces developing as numerous deep and narrow clefts, which in some cases broaden into chambers (fig. 203), so that all the green cells are bathed by

an internal atmosphere. The superficial cells (*epidermis*) of the dorsal region, discontinuous on account of the numerous clefts, may or may not contain chloroplasts. The cells of the ventral region, against the substratum, do not contain chloroplasts, and the superficial cells often give rise to simple, hairlike rhizoids that serve as holdfasts.

Antheridium. — The antheridia occur in discoid areas slightly raised above the general surface of the thallus, each antheridium standing at the bottom of a deep pit formed by the overgrowth of the surrounding tissues (fig. 204). The antheridium develops from a single superficial cell (antheridium initial), and consists of a superficial layer (wall) of sterile cells investing a compact mass of sperm mother cells (fig. 210).

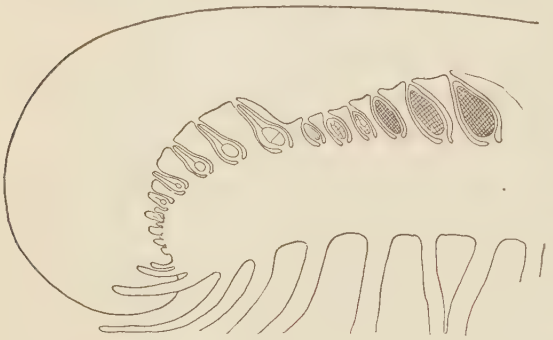
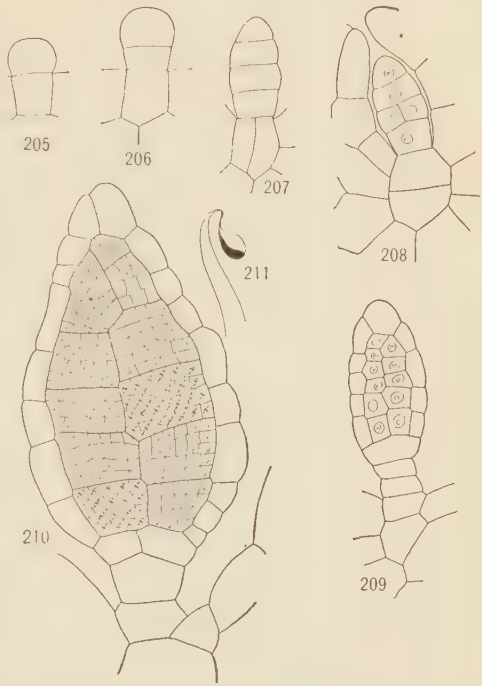


FIG. 204. — *Riccia:* section through the thallus along one of the dorsal grooves, showing the tissue at the bottom of the groove bearing antheridia (to the right) and archegonia (to the left); the rhizoids are shown arising from the lower surface of the thallus.

The antheridium initial develops a papillate protrusion, which is cut off by a transverse wall as a projecting cell. A series of transverse divisions transforms this projecting cell into a row of cells. Then vertical (*periclinal*) walls cut off central cells, which by successive divisions produce the mass of sperm mother cells (figs. 205–210). In each mother cell two sperms are formed, the oblique spindles for which are shown in two regions of fig. 210.

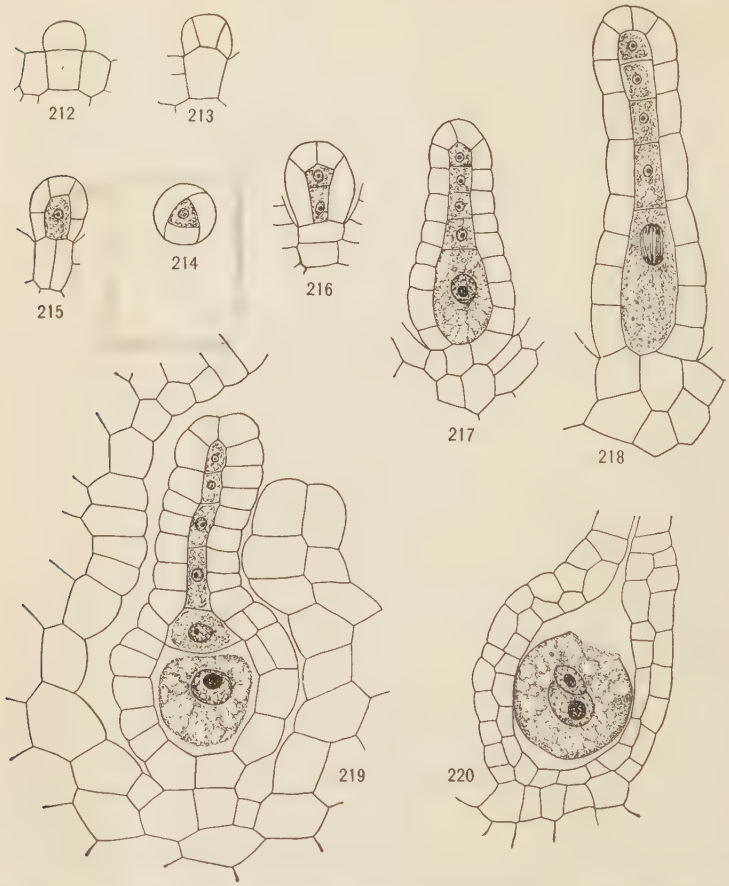
Archegonium. — The archegonia are sunk in deep pits or furrows of the thallus by the overgrowth of the surrounding tissues. The archegonium develops just as the antheridium as far as the projecting cell. This cell, however, divides by three vertical walls that surround an inner cell on all sides. A transverse division of this cell then completes the investment of a central cell. This central cell, by transverse divisions, develops the axial row, consisting of four neck canal cells, a ventral canal cell, and the egg. The investing sterile cells develop the venter and neck, the latter consisting of six vertical rows of cells (figs. 212–219).

Sporophyte. —The fertilized egg (fig. 220) produces the sporophyte (called *sporogonium* in the bryophytes), which when mature is a spherical body, consisting of a wall layer of sterile cells investing a mass of sporogenous cells (figs. 221–226). In producing this body the egg by successive divisions usually first becomes a sphere of eight cells (octants). Then periclinal (parallel with the surface) walls cut off an outer layer of cells (*amphithecium*) that forms the wall of the sporophyte. The group of inner cells is the *endothecium*, which by successive divisions produces a mass of sporogenous tissue. The cells produced by the last divisions of the sporogenous tissue are the spore mother cells, each of which produces a tetrad of spores (fig. 226), during which process the reduction in the number of chromosomes occurs. The mature sporophyte, therefore, is simply a spore case. The venter of the archegonium grows also, forming a special investing structure, the *calyptra* (fig. 225). Finally the wall layer of the sporophyte and the layers of the calyptra become disorganized, and the spores are free in the archegonial chamber. The spores upon germination produce the gametophyte body.



FIGS. 205–211. — *Riccia:* development of the antheridium; 205, first division of the superficial initial cell, the protruding cell to give rise to the antheridium; 206, first transverse division of the antheridial cell; 207, further transverse divisions; 208, the beginning of vertical walls; 209, completion of periclinal walls separating the wall of the antheridium from the spermatogenous cells; 210, an almost mature antheridium, showing the short stalk, the wall, and the mass of cubical spermatogenous cells in conspicuous blocks; 211, a sperm, showing the biciliate bryophytic type (body of sperm black; adjacent light mass is cytoplasm dragged out of the mother cell).

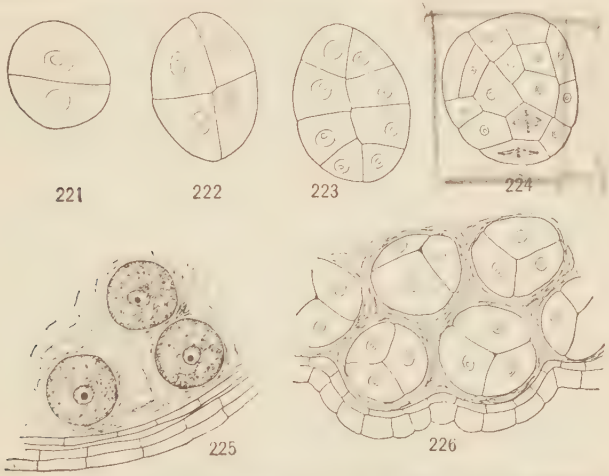
Conclusions. — The life history of the Ricciaceae suggests certain important conclusions. The sporophyte is the simplest known among



FIGS. 212–220. — *Riccia:* development of the archegonium; 212, first division of the superficial initial cell, the protruding cell to give rise to the archegonium; 213, the three vertical walls (two seen in section) investing an inner cell, the relation between the three walls being shown in the cross section, 214; 215, further development of jacket cells, completely investing a central cell (first cell of axial row); 216, first division of central cell into primary neck canal cell (upper one) and primary ventral cell; 217, further development of the jacket and axial row, the latter showing the four neck canal cells and the ventral cell (lowest and largest); 218, division of the ventral cell to produce the ventral canal cell and the egg; 219, a completed archegonium, showing neck and venter, and the axial row, consisting of four neck canal cells, a ventral canal cell, and an egg; 220, fertilization, showing male and female nuclei fusing in the egg.

liverworts, being only a spore case, and from such a structure many suppose that sporophytes of the higher plants have developed. This primitive sporophyte is dependent in a large measure upon the gametophyte for its nutrition, so that it appears simply as a spore case developed by the gametophyte.

The gametophyte, on the other hand, is far from being the simplest gametophyte known among liverworts, being quite complex in structure. The simplest liverworts should combine the simplest gametophyte with



FIGS. 221–226. — *Riccia:* development of the sporophyte (sporogonium); 221, first division of the fertilized egg (oospore), transverse to the long axis of the archegonium; 222, quadrant or octant stage; 223, still later stage; 224, the coming in of periclinal walls that separate the amphithecium (outer layer of cells) from the endothecium (after GARBER); 225, portion of sporophyte showing three of the numerous free mother cells produced, and the investing calyptra (two layers of cells); 226, tetrads (of spores) produced by the mother cells.

the simplest sporophyte, but such a combination is not known, and perhaps it no longer exists. It follows that while the history of the liverwort sporophyte may well begin with the Ricciaceae, the history of the liverwort gametophyte must begin with other forms.

Marchantiaceae. — This family includes the most highly specialized of the Marchantiales. The familiar genus *Marchantia* may be used as an illustration.

Gametophyte. — The gametophyte body is a highly developed thallus, whose dorsal region contains a series of large air chambers domed by the epidermis and containing special chloroplast-containing cells (fig. 227).

These special cells are in short and more or less branching filaments that arise from the floor of the chamber and contain the chloroplasts, and are thus freely exposed to the internal atmosphere. This remarkable apparatus is one of the specialized features of the Marchantiaceae. In the center of the epidermal dome, roofing each air chamber, there is developed a chimney-like air pore. In the ventral region the tissue is composed of colorless cells, and the ventral epidermis

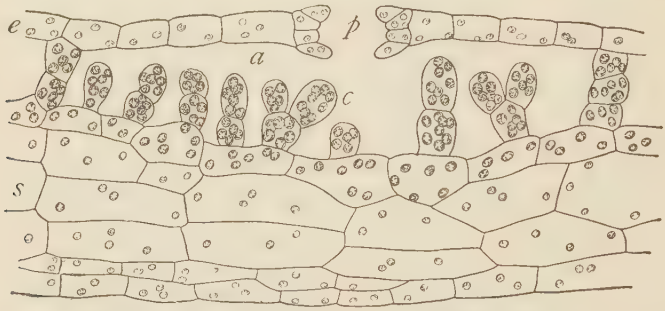


FIG. 227. — *Marchantia:* section through young air chamber (*a*), showing the special chloroplast-containing cells (*c*), the epidermal roof (*e*), and the air pore (*p*); the cells beneath the air chamber (*s*) also contain chloroplasts; the rhizoids and scales on the ventral surface are not shown.

develops two kinds of rhizoids and two longitudinal rows of scales. Upon the dorsal surface cuplike structures (*cupules*) are produced, which contain special reproductive bodies (*gemmae*), which can develop new gametophytes (figs. 228, 229). The gemma of *Marchantia* is a discoid body with two notches on opposite sides, the growing points being located at the bottom of the notches (figs. 1118, 1119).

In the development of the gametophyte body there are usually three distinct stages: (1) a filament of varying length; (2) the development in the terminal cell of an apical cell with two cutting faces,[1] by means of which the thallus begins to broaden; and (3) the development of an apical cell with three or four cutting faces, by means of which the thallus begins to thicken.

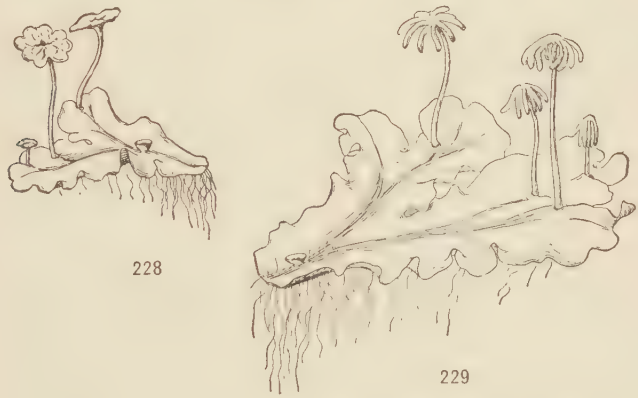
Sex organs. — The sex organs are not scattered over the dorsal surface, but are restricted to definite areas, these areas becoming disks of

[1] The current names for apical cells are somewhat confusing. For example, an apical cell with two cutting faces is called "two-sided"; one with three cutting faces a "three-sided apical cell," etc. It is evident that in each case the free surface of the cell forms another side, and that a "two-sided apical cell" is really three-sided; a "three-sided apical cell" is really four-sided, etc. That there may be no confusion, we have used the somewhat clumsy expression "an apical cell with two cutting faces," etc.

special structure (*receptacles*). In some cases the receptacles are sessile, but in *Marchantia* they become long-stalked, the archegonial and antheridial receptacles occurring on different gametophytes.

The receptacle borne by the antheridial branch is a disk with lobed margin, a growing point being at the tip of each lobe (fig. 228). Over the upper surface of this disk the antheridia occur in flask-shaped cavities formed by the overgrowth of the adjacent tissue. From the bottom of each cavity a single antheridium arises (rarely two), similar in structure to those described under Ricciaceae (figs. 205–210).

The receptacle borne by the archegonial branch is star-shaped (fig. 229), the archegonia occurring in the notches between the rays, in connection with the growing points. They arise from the upper surface



FIGS. 228, 229. — *Marchantia:* 228, thallus bearing antheridial branches and a cupule; 229, a larger thallus bearing archegonial branches and a cupule.

(morphologically) of the disk, but as this becomes the apparent lower surface by the overgrowth of the upper surface, they hang within the notches neck downward. They develop as in the Ricciaceae, but there are usually eight neck canal cells (figs. 212–219).

Sporophyte. — The sporophyte begins to develop as among the Ricciaceae, but not all of the cells of the endothecium produce sporogenous tissue. Approximately half of these cells give rise to the sporogenous tissue and spores. This means that the sporogenous tissue in the sporophyte of *Marchantia* is reduced as compared with that of the Ricciaceae. The remaining tissue of the endothecium, since it does not

produce spores, is said to be *sterile*. This sterile tissue in *Marchantia*, which was sporogenous tissue in the Ricciaceae, forms a region of the sporophyte quite distinct from the spore-producing region, so that in the mature sporophyte three regions are recognized: (1) the capsule, containing the spores; (2) the seta, a short stalk beneath the capsule, which elongates rapidly as the capsule matures; and (3) the foot, a spreading structure in which the seta ends, and which anchors the sporophyte in the gametophyte and also acts as an absorbing organ (fig. 230).

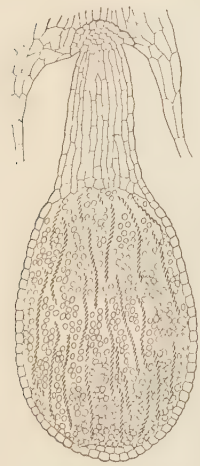


FIG. 230. — *Marchantia:* sporophyte, showing capsule (containing spores and elaters), seta, and foot (embedded in tissue of gametophyte).

The spore production of *Marchantia* is further diminished by the fact that not all the potentially sporogenous cells produce spores. Some of them become converted into curious elongated, fiber-like cells with spiral thickening (*elaters*), which by their hygroscopic movements assist in loosening up the spore mass in connection with dehiscence and scattering. The usual calyptra is formed about the developing sporophyte by the venter of the archegonium, but at maturity the capsule breaks through this by the rapid elongation of the seta. After its escape from the calyptra the capsule breaks irregularly and discharges its spores.

Conclusions. — The Marchantiales are characterized by a distinct and strong differentiation of the tissues of the gametophyte, leading to the highly complex thallus of *Marchantia*, with its specialized mechanism for photosynthesis. There is observable in the group also a distinct tendency in the sporophyte toward the sterilization of the potentially sporogenous tissue into the sterile tissue developing the seta and foot. This means that seta and foot are derived historically from sporogenous tissue. The development of the seta, moreover, is associated with the dispersal of spores, its rapid elongation freeing the capsule from the calyptra. The further sterilization of potentially sporogenous tissue in the production of elaters is another feature of the group, and is also associated with spore dispersal. On the whole, the chief distinction of Marchantiales as compared with the other groups of liverworts is the differentiation of the tissues of the gametophyte, which has reached its extreme expression in *Marchantia*.

(2) Jungermanniales

General character. — This is by far the largest group of liverworts, its members living in all conditions of moisture from very wet to very dry. They are especially abundant in tropical forests, being very common on the bark of trees (*epiphytic*) and on leaves (*epiphyllous*), while some grow on the ground. Two great groups are recognized: (1) thallose forms, whose gametophyte body is a thallus resembling that of the Marchantiales in general outline (see fig. 777); (2) foliose forms, with leafy bodies (fig. 235). However, there is complete gradation from thallus bodies, through those whose thallus is more and more deeply lobed, to those in which the lobes have become distinct leaves.

Fig. 231. — *Pellia:* thallus bearing a sporophyte with long seta (indicating also position of archegonium); the black dots on the older portion of the thallus indicate antheridia.

The most essential distinction between the two groups is based upon the position of the archegonia, which of course involves the position of the sporophytes. In the thallose forms the archegonia are on the dorsal surface of the thallus (figs. 231, 232); and on this account they are called the *Anacrogynae*, meaning archegonia not at the apex. In most foliose forms the apical cell becomes an archegonium initial; and on this account they are called *Acrogynae*, meaning archegonia at the apex (fig. 235). The acrogynous Jungermanniales are known commonly as the leafy liverworts, or sometimes as scale mosses.

Fig. 232. — *Symphyogyna:* thallus showing lobed margin and bearing two sporophytes on its dorsal surface.

In contrast with the Marchantiales, the Jungermanniales show very little differentiation of the *tissues* of the gametophyte; but they show very great differentiation in the *form* of the gametophyte.

(a) Anacrogynae

Gametophyte. — The gametophyte of the simplest Anacrogynae, such as *Aneura* and *Pellia*, are the simplest gametophytes known among

liverworts (fig. 231). They consist of dichotomously branching plates of similar cells, all containing chloroplasts, and with no differentiation of tissues into dorsal and ventral regions.

In developing from the spore, only two stages are to be observed: (1) the filamentous stage, followed by (2) the stage of the apical cell with two cutting faces. Among the Marchantiales it was noted that these two stages are followed by another, which is accompanied by a distinct differentiation of tissues. The adult thallus of *Aneura* and *Pellia*, therefore, represents an embryonic stage of the thallus of Marchantiales.

If the sporophyte of *Riccia* were combined with the gametophyte of *Pellia* in a single life history, the result would be the simplest hypothetical liverwort. Among the more highly developed Anacrogynae (*Fossombronia*, *Blasia*, *Symphyogyna*, etc.) the gametophyte becomes more complex, beginning to lobe and to develop indistinct leaves (fig. 232), and in some cases the body becomes distinctly leafy. These leafy forms are classed among the Anacrogynae, however, because the archegonia are dorsal and not terminal.

The gametophytes may be multiplied vegetatively in various ways: (1) by the death of main axes, thus isolating branches which become independent individuals; (2) by gemmae, which are many-celled bodies formed on the surface of the thallus or cut off from the margin; in *Aneura* two-celled gemmae have been seen to escape from cells of the thallus; (3) by tubers, which are special subterranean branches formed at the end of the growing season and which remain dormant until the return of favorable conditions.

Sex organs. — The sex organs occur singly or in groups on the dorsal surface of the thallus (figs. 231, 232) or of special branches. In *Aneura*, for example, the antheridia are sunk singly in pits or chambers formed by the overgrowth of the surrounding tissue (as in *Marchantia*).

The development of the antheridium is very different from that described for the Marchantiales. The projecting papillate cell, derived from the antheridium initial, divides transversely, the lower cell by successive divisions building up a stalk of varying length. The outer cell, which is to form the somewhat globular body of the antheridium, divides by a vertical wall, and this is followed by four other vertical and intersecting walls, so directed as to cut off four peripheral cells, which inclose two central cells. The peripheral cells form the wall of the antheridium, a single layer of cells in thickness; while the two central cells give rise to the sperm mother cells. The sperm has a more or less coiled body and the usual pair of long terminal cilia.

The archegonia are developed as among the Marchantiales, with three vertical intersecting walls, a cap cell, and a central cell which develops the axial row. In this case the neck canal cells are six to eight in number.

Sporophyte. — The sporophyte, even of *Aneura*, is more complex than that of *Marchantia*. Much more of the sporophyte is sterile tissue, the sporogenous tissue being still more restricted. The sterile tissue develops a foot and an elongated seta (fig. 231); and the spore output is still further reduced by the development of elaters and by the use of some of the sporogenous tissue in nourishing the functioning mother cells. In certain forms there occurs also a mass of sterile tissue projecting into the spore chamber from above (*Aneura*) or from below (*Pellia*), which, on account of its relation to the elaters that radiate from it, is called an *elaterophore*. As in *Marchantia*, the seta elongates with great rapidity when the capsule is mature. The capsule opens usually by the longitudinal splitting of the wall into four pieces (*valves*), which is a more definite and special mechanism for dehiscence than is developed among the Marchantiales.

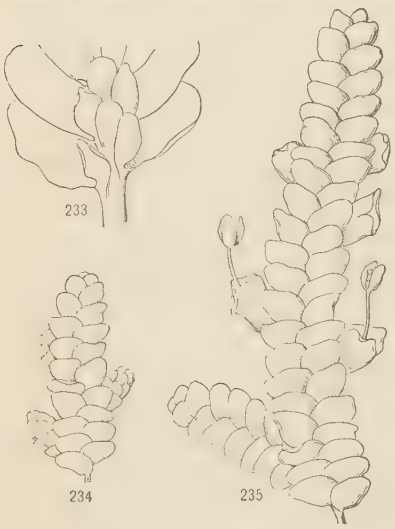
Conclusions. — The anacrogynous Jungermanniales exhibit some of the simplest gametophytes known among liverworts. There is a tendency for the gametophyte to pass from the thallose state to the leafy state, thus changing in form, but without any marked differentiation of tissues. The sporophyte is more highly developed than among Marchantiales, in the sense that there is more sterilization, more organization of the sterile tissue, a stronger development of the seta, and a more specialized dehiscence. Apparently it is a group which has retained the primitive structure of the gametophyte for a long time, but in which the sporophyte has developed rapidly. In *Pellia* and *Aneura*, therefore, we find the simplest gametophyte associated with an advanced sporophyte, the converse being true of the Ricciaceae.

(b) Acrogynae

General character. — A good representative of the leafy liverworts is *Porella*. As has been said, the Acrogynae are characterized not only by being leafy forms, but chiefly by the fact that the apical cell of special branches becomes an archegonium initial. This apical position of the archegonium and hence of the sporophyte (fig. 235) is in sharp contrast with their dorsal position among the Anacrogynae.

Gametophyte. — In the development of the gametophyte there may be three stages: (1) the filamentous stage, (2) perhaps the stage of an

apical cell with two cutting faces, and (3) the stage of the apical cell with three cutting faces. It should be noted that this is one more stage than shown by *Aneura* (see p. 102), but it is not absolutely certain that the second stage occurs, at least with any regularity. The apical cell of the last stage, cutting off three series of segments, gives rise to three rows of leaves — two dorsal and one ventral. The mature dorsiventral body consists of a distinct branching axis (stem) bearing two rows of dorsal leaves (figs. 233–235), which are usually two lobed; and one ventral row of very small leaves against the substratum (*amphigastria*), variable in form (fig. 233). The two lobes of the dorsal, chlorophyll-bearing leaves are equal or unequal; and in certain epiphytic forms the lower (ventral) lobe forms a small sac containing water.



FIGS. 233–235. — *Porella:* 233, ventral view, showing two ventral leaves (amphigastria) in the middle line, and the dorsal leaves with their ventral lobes; 234, portion of gametophyte showing three antheridial branches; 235, gametophyte with two archegonial branches bearing terminal sporophytes (opening by four valves), and three other archegonial branches.

The kinds of vegetative multiplication are the same as given under Anacrogynae (see p. 102), but the gemmae are usually simpler, often consisting of only one or two cells separating from the leaf margins.

Sex organs. — The antheridia of *Porella* are on short lateral branches, which differ very much in appearance from the sterile branches (fig. 234). They are conspicuous on account of the closely imbricated leaves, in each of whose axils there is a single, long-stalked, and globular antheridium (fig. 236). The development of the antheridium is as described under Anacrogynae (see p. 102).

The archegonia also occur on short lateral branches (fig. 235), being found in a group at the apex. This group is usually surrounded by a rosette of modified (usually enlarged) leaves. The archegonia arise from segments of the apical cell, and finally the apical cell itself becomes

an archegonium initial. The neck canal cells are six or eight in number, and the neck is almost as broad as the venter.

The two kinds of sex organs may occur upon the same plant (*monoecious*) or upon different plants (*dioecious*).

Sporophyte. — The sporophyte (sporogonium) is as described for the Anacrogynae (see p. 103), with a conspicuously elongated seta, the same reduction of sporogenous tissue, and the capsule dehiscing by four spreading valves (fig. 235).

Conclusions. — The essential contrasts between Jungermanniales and Marchantiales may be stated as follows: In Marchantiales there is (1) a differentiation of the tissues of the gametophyte, but no special differentiation of form, (2) less sterilization of potentially sporogenous tissue, (3) little or no development of the seta, and (4) irregular dehiscence of the capsule. In Jungermanniales there is (1) a differentiation of the gametophyte into axis and leaves, but little or no differentiation of tissues; (2) greater sterilization of potentially sporogenous tissue; (3) strong development of the seta; and (4) a definite dehiscence of the capsule by four spreading valves. The two groups differ also in the method of development of the antheridium. In the main, the archegonia of the two groups are similar, the axial row including six or eight neck canal cells (the exceptions being *Riccia* with four and *Sphaerocarpus* with two). The archegonium is a very persistent ("conservative") structure, but the gradual disappearance of the neck canal cells is one of the conspicuous facts in its very slow

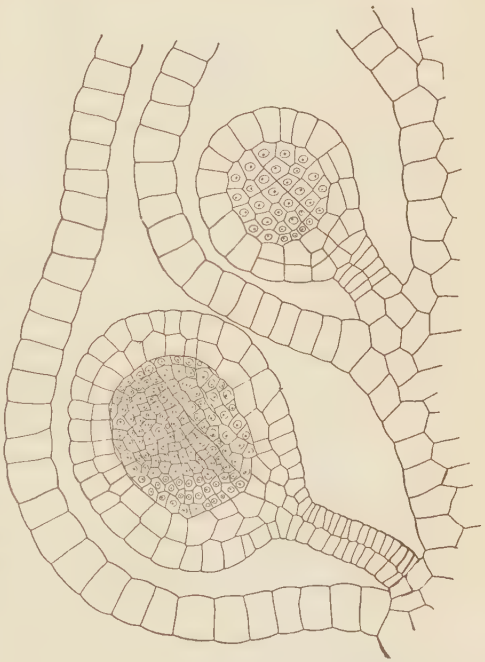


FIG. 236. — *Porella*: portion of antheridial branch showing two axillary antheridia.

evolution. It is this gradual disappearance that must be noted in connection with subsequent groups.

(3) Anthocerotales

General character. — This is a small group comprising four genera: *Anthoceros* and *Notothylas* of the temperate regions; *Dendroceros*, an epiphytic tropical genus; and *Megaceros*, a genus recently described from Java. Although few in numbers, the group is of great morphological interest on account of the claims made for it that it possibly represents the ancestral forms of pteridophytes. Its possible relation to the mosses also further emphasizes its important genetic position. It differs so much from the other liverworts as to have suggested its separation from them as a third great group of bryophytes, coordinate with liverworts and mosses. In Marchantiales and Jungermanniales there is extensive differentiation of the body of the gametophyte, either in structure or in form; but in Anthocerotales there is a simple gametophyte, while the sporophyte is the most complex among liverworts.

Gametophyte. — The body of the gametophyte is a simple thallus (figs. 239, 240), almost as simple as that of *Aneura*, and much simpler than that of *Marchantia*. The margin is often wavy, lobed, or crisped; and in *Dendroceros* the lobing in some cases suggests rudimentary leaves. The thallus matures by means of an apical cell with four cutting faces, the preceding stages appearing as usual. There are two marked peculiarities of the gametophyte body in most of the genera: (1) the usually single large chloroplast, generally in contact with or even more or less investing the nucleus; and (2) the mucilage cavities, which open by clefts on the ventral surface. In these cavities endophytic *Nostoc* colonies occur.

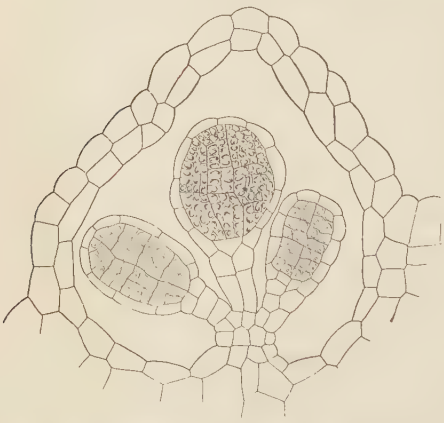


Fig. 237. — *Anthoceros:* an antheridial chamber containing three antheridia.

The sex organs are developed on the dorsal side of the thallus, but in certain features they differ strikingly from those of other bryophytes.

Antheridium. — The antheridia are embedded in the thallus and are therefore hard to detect (fig. 237). The antheridial initial is a superficial cell, but it does not develop a papillate protrusion as in the other liverworts. A transverse (periclinal) wall divides it into an outer and an inner cell. In the other groups the outer cell develops the antheridium, but in Anthocerotales the antheridium is developed from the inner cell. By a succession of anticlinal and periclinal divisions, the outer cell produces two layers of cells, which form an outer wall or roof to the antheridial chamber.

The inner cell develops one to several antheridia. The method of development of an antheridium, whether directly from the inner cell or from one of its daughter cells, is as follows: two vertical walls at right angles to each other result in four cells; transverse walls result in several tiers of four cells each; periclinal walls in the upper tiers cut off an outer wall layer and an inner group of spermatogenous cells; and the lower tiers (sometimes only the lowest) develop a more or less elongated stalk. The antheridium or group of antheridia thus produced lie in what may be called an antheridial chamber (fig. 237).

Archegonium. — The archegonia also are in the tissue of the thallus, in this respect resembling the archegonia of pteridophytes (fig. 238). In all other bryophytes they are entirely superficial structures. As a result of this relation to the thallus, there are no sterile jacket cells (neck and venter) very distinct from the adjacent cells of the thallus. The essential part of an archegonium, however, is the axial row, and in the Anthocerotales this is the only distinct structure.

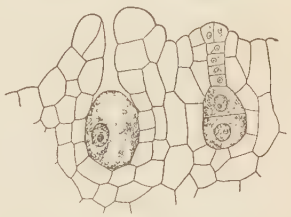


FIG. 238. — *Anthoceros:* archegonia, showing "embedded" character; in the archegonium to the right the complete axial row is shown (beginning below, the cells are the egg, ventral canal cell, and four neck canal cells) capped by the neck cells (two visible); in the archegonium to the left, the neck cells have been thrown off, the canal cells have disorganized, and there is a passageway open to the egg, which is ready for fertilization.

The general outline of development of this axial row is as follows: a superficial cell divides transversely, giving rise to outer and inner cells; the outer cell divides transversely, giving rise to the *cap cell* and the *primary neck canal cell;* the inner cell is the *primary ventral cell;* the primary neck canal cell, by two successive divisions, develops a row of four neck canal cells; the primary ventral cell, by a single transverse division, forms the ventral canal cell and the egg. At maturity the cap cells are thrown off, the neck and ventral canal cells break down, and a broad canal is open to the egg (fig. 238).

Sporophyte. — The sporophyte of Anthocerotales deserves special attention on account of its structure and on account of its degree of independence (figs. 239, 240). The outline of its development is as follows: the fertilized egg divides by a vertical wall (transverse in other bryophytes); subsequent transverse and vertical walls result in three tiers of four cells each; the three tiers produce foot, seta, and capsule. The innermost tier develops a foot which penetrates the thallus by rhizoid-like processes, and finally becomes a large bulbous structure (fig. 241). The middle tier, which also contributes somewhat to the foot, develops the so-called intermediate zone, corresponding in position to the seta of other groups. It is a region of active cell-division, continually adding to the capsule below, which thus becomes an elongated structure by basal growth (as distinct from apical growth). This growth may not continue long, resulting in a short capsule (*Notothylas*, fig. 240); or it may continue long enough to result in a much elongated linear capsule (*Anthoceros*, fig. 239). Where the sporophyte (sporogonium) emerges from the thallus, a tubular sheath is developed around its base by the tissue of the thallus.

FIGS. 239, 240. — *Anthocerotales:* 239, thallus of *Anthoceros* bearing sporophytes; the two sporophytes to the right show the dehiscence by two valves, leaving the columella exposed; 240, thallus of *Notothylas* bearing sporophytes.

Capsule. — The development of the outermost tier in capsule formation is especially noteworthy. By a series of transverse walls a number of tiers of cells is produced, and periclinal walls cut off a peripheral layer of cells (amphithecium) inclosing a group of central cells (endothecium). Among the Marchantiales and Jungermanniales there is the same setting apart of two regions, the amphithecium producing the capsule wall, and the endothecium developing the sporogenous tissue. Among the Anthocerotales, however, the two regions develop in a very different way. The endothecium does not develop sporogenous tissue, but forms a central axis of sterile tissue (*columella*), which in *Anthoceros* usually shows sixteen cells in cross section. By periclinal walls, the amphithecium becomes two-layered, and the inner layer is the sporogenous tissue, which thus caps the columella in a domelike layer;

later the sporogenous tissue becomes two layers of cells. The outer layer of the amphithecium develops a capsule wall of four or more layers, the outermost one being the epidermal layer, consisting of elongated narrow cells and containing stomata similar to those of vascular plants. The stomata are related to the fact that the wall layers beneath the epidermis are chlorophyll tissue, giving to the sporophyte the ability to manufacture food. The intermediate zone adds continuously new capsule regions below; therefore in a longitudinal section of a capsule the whole sporogenous series may be seen, from one-layered sporogenous tissue below, through two-layered sporogenous tissue, mother cells, and tetrads, to mature spores above (fig. 241). The capsule dehisces by splitting into two valves, which separate downwards as the spores mature, leaving the spores exposed upon the columella (fig. 239).

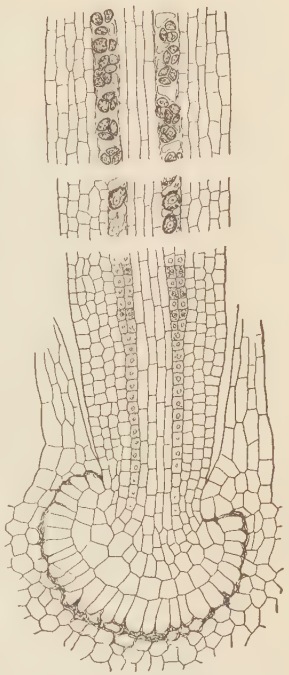


FIG. 241. — *Anthoceros:* longitudinal section through portions of a sporophyte, showing bulbous foot embedded in the gametophyte; above the foot is the zone of actively dividing cells elongating the sporophyte; the base of the capsule shows the peripheral chlorophyll tissue, the sporogenous tissue (at first one layer of cells, then dividing to form two layers), and the columella; section from middle region showing spore mother cells with sterile cells between; section from upper region showing tetrads and sterilized sporogenous cells.

In many cases some of the sporogenous cells do not form spores. These sterile groups of cells break up the continuous mass of sporogenous cells into more or less separated groups. This tendency to break up the sporogenous tissue into separate smaller masses by intervening sterile tissue is an important fact, which will be referred to later. These sterilized and somewhat modified sporogenous cells are called elaters, but they are different from those found among Marchantiales. This green sporophyte, with its sterile and elongating axis, and its sporogenous tissue broken up into smaller masses, is very suggestive of a possible relation to the completely independent sporophyte of the pteridophytes.

Conclusions. — Among the Anthocerotales there is a remarkable association of a primitive type of gametophyte with a highly developed

sporophyte. In considering the sporophytes of liverworts in general, it is evident that from *Riccia* to *Anthoceros* there is a progressive sterilization of sporogenous tissue, the sterilized tissue forming the vegetative structures. Among the Anthocerotales three additional features of the sporophyte are noteworthy: (1) the beginning of independence by the development of green tissue; (2) the beginning of sporangia by the breaking up of a continuous sporogenous mass into separate smaller masses; (3) the establishment of a sterile axis by the transfer of the sporogenous tissue to the outer region of the capsule, which suggests the beginning of a region for the development of vascular tissues and the beginning of superficial sporangia.

It should be understood clearly just what is meant by such a statement as that the Anthocerotales have certain features suggestive of the pteridophytes. It does not mean that the pteridophytes have been derived from the Anthocerotales or from any of the bryophytes. It means simply that the sporophyte of the Anthocerotales represents a stage of progress like one through which the pteridophytes may have passed during their evolution. The plant groups as we know them now certainly did not give rise to one another, but they can be used to suggest general stages of progress, of whose real details and connections we know nothing.

2. MUSCI

General character. — This is the great group of bryophytes, both in numbers and in specialization. While the liverworts may be the more interesting from the standpoint of suggestions as to phylogeny, the mosses are the representative bryophytes in our present flora. For so great a group it is very well defined and consistent. Mosses are widely distributed, being found in all habitats except salt water, and are especially conspicuous in colder regions (alpine and arctic), where they form a prominent feature of the vegetation. They seem to have been derived from liverworts, and their sporophyte characters, at least, suggest a possible connection with Anthocerotales; while in certain features of the gametophyte the resemblance to Jungermanniales is more evident. Three groups are recognized: (1) *Sphagnales*, (2) *Andreaeales*, and (3) *Bryales*.

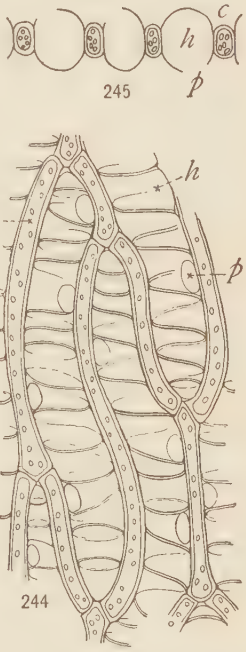
(1) Sphagnales

General character. — These are the bog mosses, all of which belong to the single genus *Sphagnum*. They are large, pale mosses, character-

istic of the swampy regions of higher latitudes, where they often fill up bogs and form peat, whence they are often called peat mosses.

Gametophyte. — The gametophyte begins as a filament (fig. 242), and then by means of an apical cell with two cutting faces develops as a simple flat thallus with rhizoids (fig. 243), just as in the simpler liverworts. The moss character appears in the development from this liverwort-like thallus of an upright leafy branch (fig. 243). This radial leafy branch, from a dorsiventral body, is called variously the adult shoot, the gametophore, or simply the leafy branch. The name gametophore is used because this branch bears the sex organs, just as in *Marchantia* the sex organs are borne on erect but leafless branches.

FIGS. 242, 243. — *Sphagnum:* 242, young gametophyte, showing the filament arising from the spore, a rhizoid, and the thallus beginning to develop by an apical cell; 243, mature thallus, with rhizoids, producing leafy branches. — After SCHIMPER.



FIGS. 244, 245. — *Sphagnum:* 244, surface view of cells of leaf, showing the narrow elongated cells (*c*) containing chloroplasts, and the less numerous hyaline cells (*h*) with pores (*p*); 245, portion of cross section showing same features.

The leafy branch develops by means of an apical cell with three cutting faces, and hence there are three vertical rows of leaves. These branches are densely leafy and profusely branching, forming terminal tufts (fig. 246).

The leaves at first have similar cells, but later there is a striking differentiation, certain of the cells becoming enlarged, hyaline, and perforate (figs. 244, 245). It is this abundance of hyaline cells and paucity of chlorophyll-containing cells that give a pallid look to the leaves.

FIG. 246. — *Sphagnum:* terminal cluster of antheridial branches.

The axis of the leafy branch is differentiated into three regions: (1) a cortex of empty and perforate cells, like the hyaline cells of the leaf; (2) a cylinder of elongated cells with thick walls and small caliber (*prosenchyma*); and (3) a pithlike axis.

There are no special structures for vegetative multiplication, but great masses of individuals are formed by the indefinite growth and branching above, accompanied by dying off below.

Antheridium. — The antheridia occur on special densely leafy branches resembling small catkins (fig. 246). The leaves also usually differ in color from the ordinary leaves, and in the axil of each there is a solitary globular and long-stalked antheridium (fig. 247), just as in *Porella* (see p. 104). These antheridia develop by means of an apical cell with two cutting faces, the lower segments forming the stalk, and the upper segments forming the capsule, which is initiated by a series of periclinal walls that cut off the peripheral wall layer from a central spermatogenous group of cells. The antheridium opens by irregular lobes and discharges the two or three-coiled biciliate sperms.

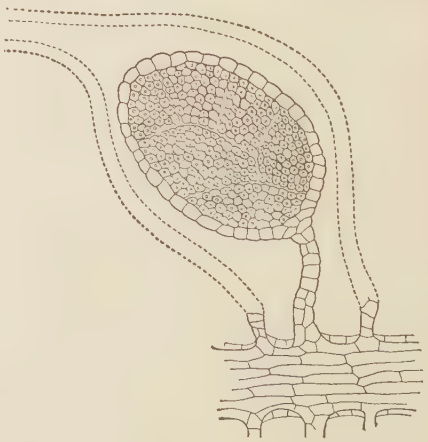


FIG. 247. — *Sphagnum:* an antheridium arising on branch between two leaves, showing the slender stalk and the globular head; the latter consisting of a wall (a single layer of cells) investing a mass of spermatogenous cells (in which blocking can be distinguished).

Archegonium. — The archegonia occur at the apex of short branches, at the top of the plant (figs. 248, 249). They are stalked and free, and develop as in the acrogynous Jungermanniales, the archegonium initials being segments of the apical cell, which itself finally becomes an

initial. The mature archegonium is stalked, with a massive venter, a long and often twisted neck, and numerous neck canal cells (fig. 249).

Sporophyte. — The sporophyte (fig. 250) develops at first by a series of transverse walls until a short filament is formed, which later becomes massive by means of vertical walls. The upper tiers develop the capsule, which is organized as in *Anthoceros*, with the endothecium developed as the axial columella, with the sporogenous tissue cut off as an inner layer (becoming four layers) of the amphithecium and capping the columella like a dome, and with a wall of five to seven layers. These *Anthoceros*-like features are further emphasized by the large bulbous foot and the rudimentary seta, which is only a necklike connection between capsule and foot, and is often called the neck. Very important differences, however, are as follows: (1) there is no such development of chlorophyll tissue in the wall of the capsule as characterizes *Anthoceros;* (2) the neck is not a growing region, and hence the capsule does not elongate; and (3) the capsule dehisces by a definite lid (*operculum*), which is distinctly a moss character. As in all bryophytes, during the development of the sporophyte the venter of the archegonium develops the encasing calyptra, which in *Sphagnum* is ruptured by the growing capsule.

FIG. 248. — *Sphagnum:* stem bearing a terminal cluster of sporophytes, showing the position of archegonia.

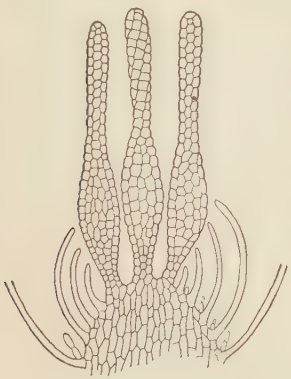


FIG. 249. — *Sphagnum:* surface view of three archegonia; the middle archegonium shows the spiral direction of the cell rows of the neck. — After SCHIMPER.

A peculiar feature of *Sphagnum* is the *pseudopodium*, which is a structure replac-

ing in function the suppressed seta. It is formed by the elongation of the axis of the leafy branch beneath the sporophyte, and as it bears the capsule at its summit, it resembles an ordinary elongated seta (fig. 250). Of course the foot of the sporophyte is embedded in its tip.

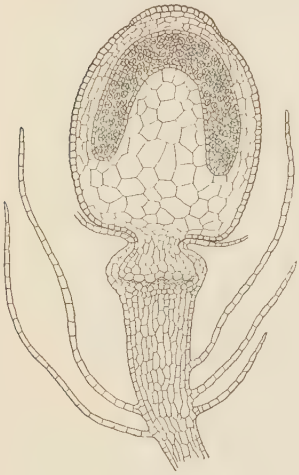


FIG. 250. — *Sphagnum:* sporophyte, showing the globular capsule with operculum (lid) and dome-shaped mass of sporogenous tissue (in tetrad stage), the very short necklike seta, the bulbous foot embedded in the apex of the leafy axis (gametophyte), which is extended beyond the leaves to form the stalklike (seta-like) pseudopodium.

Conclusions. — The Sphagnales present a remarkable mixture of liverwort and moss characters. The simple thallus body of the gametophyte resembles that of the anacrogynous Jungermanniales; the special leafy sex branches suggest the acrogynous Jungermanniales; while the sporophyte is organized as in the Anthocerotales. On the other hand, the erect leafy branches of the gametophyte and the operculum of the sporophyte are both distinctly moss characters. In addition to these characters in common with liverworts and true mosses, *Sphagnum* possesses other characters peculiar to itself.

It was remarked that the simplest conceivable liverwort would be produced by combining the gametophyte of *Pellia* with the sporophyte of *Riccia*. So in producing *Sphagnum*, one might imagine a combination of the gametophytes of the two groups of Jungermanniales with the sporophyte of *Anthoceros*.

The features of *Sphagnum* that distinguish it from true mosses in general are (1) the thallose gametophyte, (2) the axillary antheridia, (3) the dome-shaped sporogenous tissue derived from the amphithecium, and (4) the pseudopodium.

Such a form is often called a *transition* form, but better a *synthetic* form, for it combines the characters of several groups.

(2) ANDREAEALES

General character. — This group comprises a single genus (*Andreaea*) of siliceous rock mosses. *Sphagnum* is hydrophytic, but *Andreaea* is very xerophytic.

It is introduced here partly to illustrate the possible effect of changed conditions upon structure, but chiefly to illustrate another synthetic form.

Gametophyte. — The gametophyte develops first as a mass of cells (*primary tubercle*). From the superficial cells of the primary tubercle extensively branching filaments arise, which represent the *protonema* of the true mosses, as contrasted with the thallus of *Sphagnum* and the liverworts. The branches of the filament that enter the rock crevices are rhizoids; those that remain exposed to the light are green and may assume any one of three forms dependent upon conditions: (1) they may remain filamentous; (2) they may form flat plates; or (3) they may form cylindrical masses. The leafy branch may arise from any of these three forms. Arising from filaments, it resembles a true moss; arising from a plate of cells, it resembles *Sphagnum*.

Sex organs. — The antheridia occur at the apex of a special branch, involving the apical cell; this resembles true mosses and not *Sphagnum*. In form, however, the antheridium is globular and long-stalked, resembling *Sphagnum* and not the true mosses. The archegonia also occur at the apex of a special branch, this character being common to leafy liverworts, sphagnums, and true mosses.

Sporophyte. — The sporophyte presents the great peculiarities of the group. The sporogenous tissue is cut off from the endothecium as the outermost layer of cells, a feature resembling true mosses but not *Sphagnum*; but the sporogenous tissue caps the columella like a dome, a feature resembling *Sphagnum* but not true mosses. A pseudopodium develops instead of a seta, as in *Sphagnum*. The dehiscence of the capsule is very peculiar, for instead of the operculum of other mosses, there are four vertical slits that do not reach the apex, recalling the four valves of the capsule of Jungermanniales. In fact one of the Jungermanniales (*Symphyogyna*) has just this dehiscence by means of four vertical slits.

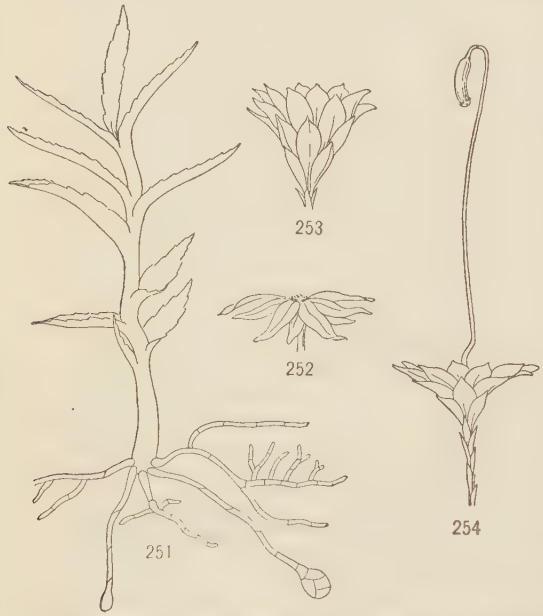
Conclusions. — The combination of characters may be summarized as follows: the gametophyte is either thallose, as in *Sphagnum*, or partly filamentous, as in true mosses; the antheridia are terminal, as in true mosses, but long-stalked and globular, as in *Sphagnum*; the sporogenous tissue is derived from the endothecium, as in true mosses, but caps the columella, as in *Sphagnum* and *Anthoceros*; the capsule dehisces by four slits or valves, as in Jungermanniales, and not by an operculum, as in other mosses; a pseudopodium is developed, which is a feature of *Sphagnum*, but not of true mosses.

(3) Bryales

General character. — This is the great assemblage of mosses, distinguished from all others as true mosses. It includes the most highly organized bryophytes, and is their most representative group, but it seems to be a closed line; that is, it has given rise to no higher groups. Although a vast group, it is so uniform in general structure that a single account will suffice.

Gametophyte. — The gametophyte is a branching filament (*protonema*, fig. 251), which is the equivalent of the thallus of *Sphagnum*

and the liverworts. In these groups the thallus in its development passes through two or three stages, the first one being filamentous; in the true mosses this earliest filamentous stage persists. This fact is associated with the development of the erect leafy branch (gametophore) characteristic of mosses. With green tissue displayed by erect branches the display of green tissue by the thallus body declines, and the thallus finally remains in an embryonic stage. Although the leafy branch is the conspicuous part of mosses, it should not be thought of as the gametophyte, but as a branch of the gametophyte (fig. 251). In certain mosses, known as reduced forms, this branch is not so prominent in its display of green tissue, only a few leaves appearing; in fact it may bear only a single scale leaf in addition to the sex organs.



FIGS. 251–254. — *True moss:* 251, leafy branch arising from protonema and putting out rhizoids; a well-developed "resting bud" is shown; 252, terminal rosette containing sex organs; 253, rosette containing archegonia; 254, a sporophyte arising from a cluster of archegonia.

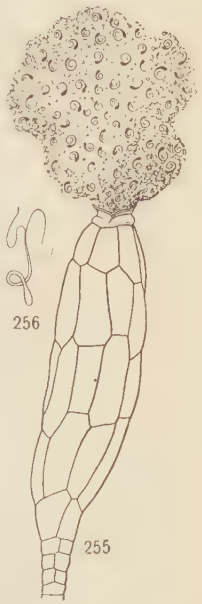
The leafy branch develops by means of an apical cell with three cutting faces. The segments are cut into outer and inner cells, the former, for the most part, developing the leaves; the latter the axis. The leaves usually consist of a single plate of green cells, often thickened in the middle so as to resemble a midrib.

Vegetative multiplication. — The power of vegetative multiplication is remarkably developed. The leafy branch bears the sex organs above the moist substratum, so that the conditions are not favorable for swimming sperms. As a consequence, fertilization in many mosses

is rare, and in some cases even sex organs are rare. Therefore, it is probable that reproduction is chiefly by vegetative multiplication, which may occur as follows: (1) the isolation of branches by the death of older axes; (2) the production of gemmae; (3) the production of resting buds on the protonema, which seem to be only arrested branch buds (fig. 251); and (4) under appropriate conditions, the development of a new protonema from any part of the leafy branch, or from fragments of leaves and axes. It follows that a gametophyte once started may propagate indefinitely.

Sex organs. — The sex organs are grouped at the end of the main stem or of its branches. Around this terminal cluster of sex organs the leaves usually become modified in form and sometimes in color, forming a sheath or a rosette (figs. 252, 253), the whole being the so-called moss "flower," a most inappropriate name. The antheridia and archegonia may occur together in the same cluster, or they may be in separate clusters, and sometimes they are intermixed with multicellular hairs (*paraphyses*).

In the true mosses the antheridia hold the same relation to the apical cell that the archegonia hold in the acrogynous Jungermanniales and in Sphagnales. The antheridium initials are segments of the apical cell, and the apical cell itself usually becomes an initial. The growth is by means of an apical cell with two cutting faces, and the form is usually club-shaped, with a stalk of variable length. In discharging the sperms, the cells at the apex separate, the mother cells are discharged *en masse*, and then the tip cells spring together again, so that empty but complete antheridia are often observed (fig. 255).



FIGS. 255, 256. — *True moss:* 255, an antheridium discharging sperm mother cells; 256, a single sperm. — After SACHS.

The archegonia differ from those of the liverworts in one important particular. The central cell (*primary oogenous cell*) does not form all of the axial row, which is added to by successive divisions of the cap cell. The mature archegonia of mosses are usually more conspicuously stalked than in the other groups, with more massive venter, and with smaller, more numerous, and more ephemeral canal cells (fig. 257).

Sporophyte. — The sporophyte is the most characteristic and complicated structure in true mosses (fig. 254). As it develops from the fertilized egg, the venter and stalk of the archegonium develop a remarkable calyptra, which enlarges very much, but is finally ruptured near the base by the growing sporophyte and is carried up as a cap or hood on the top of the capsule. The first division of the egg is transverse, and an apical cell with two cutting faces is developed in the outer cell or in some one of its early progeny. A variable number of segments is cut off (fig. 258), resulting usually in a much elongated embryo. In the upper end of the embryo the usual differentiation into amphithecium and endothecium occurs; the former develops into several layers, the latter into quite a mass of cells (figs. 259, 260). The sporogenous tissue is cut off late from the periphery of the endothecium, but does not cap the columella, which extends completely through the capsule as an axis (figs. 261, 262). The sporogenous tissue becomes two layers of cells, the mass not being dome-shaped, as in *Anthoceros* and *Sphagnum*, but barrel-shaped. Among bryophytes, the sporogenous tissue, therefore, reaches its greatest relative reduction in true mosses.

FIG. 257. — *True moss:* an archegonium, showing the conspicuous stalk, the long neck, and the axial row (composed of egg, ventral canal cell, and numerous disorganized neck canal cells).

Capsule. — The final structure of the capsule is extremely complex, and a longitudinal section may be outlined as follows (fig. 263), beginning with the outside: (1) the epidermal layer, (2) several layers of wall cells, (3) a region of intercellular cavities traversed by threads of chlorophyll tissue, (4) a tapetal layer (see p. 126); these four regions belong to the amphithecium. The endothecium is differentiated as follows: (5) the two layers of sporogenous cells, (6) an inner tapetal layer, (7) a region of intercellular cavities traversed by threads of chlorophyll tissue, (8) the columella. The inner region of cavities (7) is present only in such peculiarly organized forms as *Polytrichum*. At the maturity of the capsule the water fails, all the

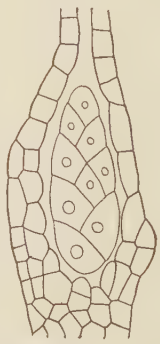
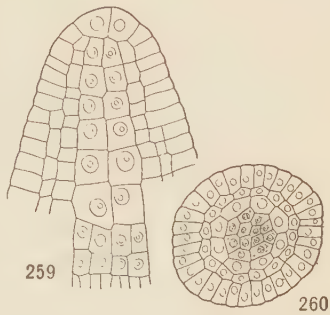


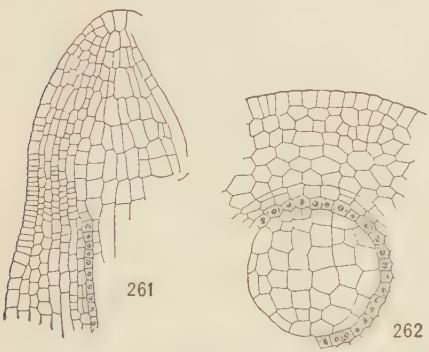
FIG. 258. — *True moss:* a young sporophyte, showing the work of the apical cell. — After BARNES and LAND, ined.

tissues between the epidermal layers dry up, and the spores are free in the large cavity.

Operculum and peristome. — The development of the operculum is complicated (fig. 264). It is sometimes early differentiated from the capsule by a shallow depression where a narrow zone of cells forms a plane of cleavage. Above and below this cleavage plane the tissue grows more rapidly, resulting in two evident rings; the upper one is the *annulus*, the lower one the *rim*. The rim is the more or less thickened top of the urnlike capsule; but the annulus is a definite ring which often becomes detached. The sterile apex is at first solid, the center, occupied by endothecial tissue, being a continuation of the columella. The sporogenous tissue and the region of cavities end just opposite the cleavage plane, so that they are not represented at the apex. The amphithecial region of the apex develops in a peculiar way. The outer walls of one of the inner layers of cells (usually the innermost) become much thickened; this layer is anchored to the rim below by a plate of thick-walled cells. When the tissues of the capsule dry out, all the tissues within the operculum, except this heavy layer of walls, disappear, and the operculum slips off like a cap, leaving these heavy walls in a conical group of toothlike projections (*peristome*) anchored below to the rim. Sometimes there are two sets of peristome teeth, in which case both the inner and the outer walls of the peristome-forming cells become thickened. There are many variations in peristomes in detail of development and in pattern.



FIGS. 259, 260. — *True moss:* 259, longitudinal section of tip of young sporophyte, showing differentiation into amphithecium (three layers of cells below) and endothecium; 260, cross section of the same, the cells of the endothecium shaded. — After CHAMBERLAIN.



FIGS. 261, 262. — *True moss:* 261, longitudinal section of tip of sporophyte showing (below) the several wall layers (amphithecium), the sporogenous layer (shaded) cut off from the endothecium, and (above) the beginning of the operculum; 262, cross-section of same, showing (beginning at center) columella, single layer of sporogenous cells, and eight or nine wall layers developed from the amphithecium. — After CHAMBERLAIN.

Apophysis. — The lower part of the capsule does not always develop sporogenous tissue; it is then characterized by a greater display of chlorophyll tissue and stomata

(fig. 263). This principal chlorophyll-bearing region of the sporophyte (*apophysis*) often is conspicuous, and sometimes becomes remarkably expanded.

Seta. — The seta is highly organized, with a central strand of elongated cells (not vascular); in fact it is the most highly differentiated axial structure below vascular plants (see figs. 1013–1016).

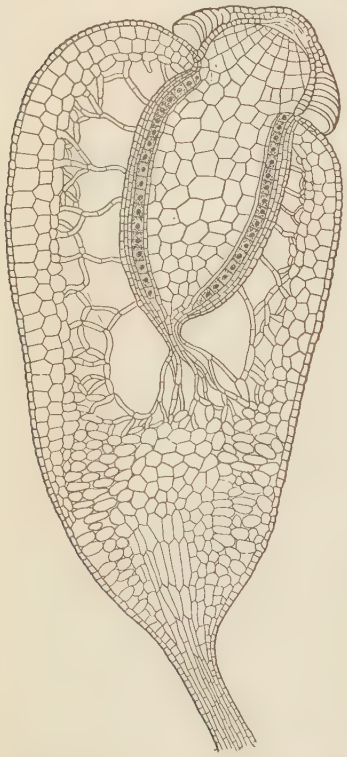


FIG. 263. — *True moss:* longitudinal section through a mature capsule, showing operculum, peristome, columella, sporogenous tissue, complex wall of the capsule (conspicuous in which is the air-chamber region), and the apophysis (the region between the seta and the bottom of the air-chamber region).

The great groups. — The principal groups of so large an assemblage of forms as the true mosses should be indicated, but it should be understood that they are extremely unsatisfactory, because they are very

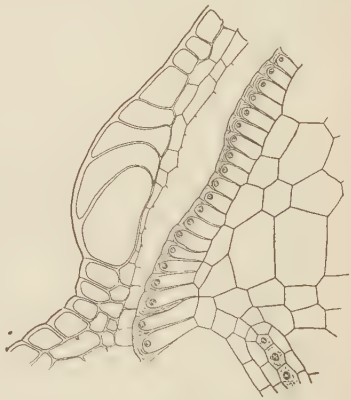


FIG. 264. — *True moss:* structure of the operculum in longitudinal section; large cells in epidermal row belong to annulus; within are the thickening walls (shaded) of a layer of amphithecial cell, to form the peristome, which is anchored by special cells to the rim of the capsule below the annulus; three sporogenous cells (shaded) represent the top of the sporogenous layer, to the left of which is the large air-chamber developed in the amphithecium. — After CHAMBERLAIN.

artificial. The two main divisions are (1) *Cleistocarpae* (or cleistocarps), characterized by the absence of an operculum, and hence with no peristome, the capsule opening by irregular rupture or decay; and

(2) *Stegocarpæ* (or stegocarps), characterized by an operculum and generally a peristome. The stegocarps are much the more numerous and representative mosses, comprising two groups: (*a*) *Pleurocarpæ*, with the archegonia (and of course the sporophyte) terminal on short lateral branches; and (*b*) *Acrocarpæ*, with the archegonia terminal on the main axis. Highest among the stegocarps is the great family Polytrichaceæ, of unusual size and complexity in both leafy branch and sporophyte. The leaves have a specially organized chlorophyll tissue; the central region of the stem and seta almost suggest conducting tissue; and there are distinct leaf traces.

Conclusions. — Some of the general conclusions as to bryophytes may be summarized as follows: The gametophyte begins as a simple thallus body and culminates as a filamentous body bearing erect leafy branches. This is the gametophyte at its best, for in the higher groups it is much less highly developed. Such a gametophyte introduces conditions unfavorable for the functioning of sperms.

The sex organs are fairly constant, the archegonia more so than the antheridia. There is a shifting in position from a general distribution over the dorsal surface of the gametophyte to special regions, and finally to the tips of leafy axes, and in this terminal position the archegonia preceded the antheridia. The conspicuous exception in the development of sex organs and their relation to the gametophyte is found in Anthocerotales, in which they are embedded in the tissue of the thallus, the antheridium developing from the inner cell resulting from the periclinal division of the initial, and the archegonium being invested by the growing tissue of the thallus. This relation of the archegonium to the tissue of the thallus is characteristic of pteridophytes.

The sporophyte begins as a simple spore case, being all sporogenous except the single layer of wall cells. But progressive sterilization of potentially sporogenous tissue proceeds through all bryophytes, culminating in the true mosses, in which the sporogenous tissue is much reduced in extent and appears late, and the great bulk of the sporophyte consists of sterile tissue, from which develops a foot, a highly differentiated seta, and a capsule of remarkable complexity.

The sporophyte is dependent upon the gametophyte in all bryophytes, but there is evidently a tendency towards independence, as shown by the development of chlorophyll tissue, which reaches its highest expression in Anthocerotales and in the apophysis of certain mosses.

CHAPTER III — PTERIDOPHYTES

Introductory. — The gap between bryophytes and pteridophytes is perhaps the greatest in the plant kingdom. To pass from the leafless, dependent sporophyte of bryophytes to the leafy, independent, vascular, root-bearing sporophyte of pteridophytes is a very sudden and complete change. One of the great problems in the evolution of plants is to explain how the leafless sporophyte became a leafy one; and a part of the problem is to discover the most primitive sporophyte among pteridophytes, concerning which there is great diversity of opinion. For convenience of presentation, the sequence of groups suggested by BOWER will be used.

(1) LYCOPODIALES

General character. — The club mosses are widely distributed and comprise about one eighth of the living pteridophytes. The group includes four living genera and also numerous extinct forms, among which are some of the oldest known vascular plants. The three genera *Lycopodium*, *Phylloglossum*, and *Selaginella* are evidently closely related, forming a very natural group, while the fourth genus, *Isoetes*, has given rise to much discussion as to its affinities.

Lycopodium

General character. — This genus, comprising about 100 living species, is in all probability one of the oldest living genera of vascular plants, and possibly is represented in the Paleozoic. It deserves a somewhat full description, as it is possibly the best living representative of the earliest forms of vascular plants.

Sporophyte. — The sporophyte in its simplest form is a simple stem covered with very numerous small leaves, and on the upper side of each leaf there is a single large sporangium (fig. 265). Leaves bearing sporangia are called *sporophylls*, and therefore this simplest vascular sporophyte is a simple leafy stem, with every leaf a sporophyll. An assemblage of sporophylls is a *strobilus*, and therefore this primitive

sporophyte is a strobilus. The problem, therefore, is how such a leafless sporophyte (sporogonium) as occurs among bryophytes could become a strobilus or rather a strobiloid body.

An explanation of the origin of this body has been suggested by BOWER'S theory of the strobilus. The partially independent sporophyte of *Anthoceros* is selected as illustrating a possible ancestral condition of vascular plants at the level of bryophytes, and the possible successive changes are outlined as follows: (1) the sporogenous tissue becomes more and more superficial (a change begun when the sporogenous tissue is transferred from the endothecium to the amphithecium); (2) the continuous sporogenous layer becomes broken into separate masses by intercalated sterile tracts (a condition present among Anthocerotales); (3) the separated sporogenous masses become more superficial, resulting in an alternation of green tissue and sporogenous tissue; (4) the intervening green tissue develops green expansions (small

FIG. 265. — *Lycopodium pithyoides:* a sporophyte consisting of a branching stem covered with small leaves, each leaf bearing a sporangium; the simplest type of *Lycopodium* sporophyte, except that it is branching.

leaves), each one having at base a mass of sporogenous tissue (*sporangium*). This final structure is the simple *Lycopodium* body just described. It is the so-called *Selago* type, in which all or nearly all the leaves are sporophylls, and hence practically the whole body is a strobilus. It must be understood that this proposed origin of the *Lycopodium* sporophyte is simply a theory, but it is a very suggestive one.

The more complex sporophytes of *Lycopodium* are branching bodies (fig. 265). There is a gradual sterilization of the lower sporophylls, which thus become simply foliage leaves. Finally the sporophyte becomes differentiated into two distinct regions: that bearing foliage leaves and that bearing sporophylls. The sporophylls finally become quite different in appearance from the foliage leaves and are organized into a compact strobilus, which is sometimes separated from the branching leafy body by a long stalk bearing only rudimentary leaves (fig. 266).

FIG. 266. — *Lycopodium complanatum:* a sporophyte showing distinct differentiation between foliage region and strobilus.

Vascular system. — The anatomy of the stem emphasizes further the primitive character of this sporophyte. A cross section shows two regions: the *cortex*, an outer region of living cells; and the *central cylinder* or *stele*, in which the vascular system (conducting system) is developed. The vascular system has been found to be of great importance in any study of the evolution of vascular plants, and, therefore, the outline of its history must be indicated. In the simpler lycopodiums, or in young stems, the vascular system of the stem forms a solid axial cylinder, in which the *xylem* (the group of water-conducting vessels) is completely surrounded by the *phloem*

(food-conducting cells), such an arrangement being called the *concentric* arrangement. This most primitive vascular system of the stem, therefore, consists of a single, solid cylinder with concentric xylem and phloem (commonly spoken of as a concentric cylinder), to which type the name *protostele* has been given. In mature stems of *Lycopodium*, the solid xylem strand may divide into branches which run through the stele as several strands separated by pithlike tissue (fig. 267). From the vascular cylinder strands pass out through the cortex, where they are called *leaf traces* (fig. 267), and enter the leaves, where they become continuous with the *veins*.

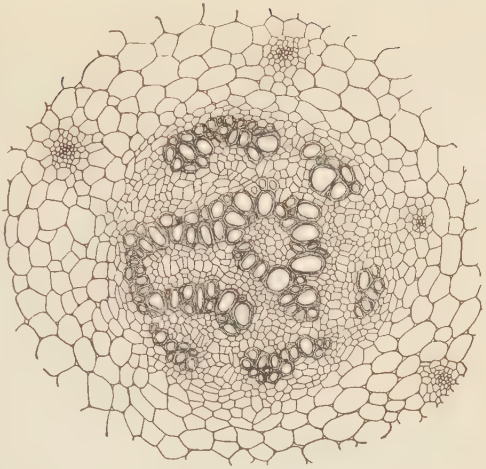
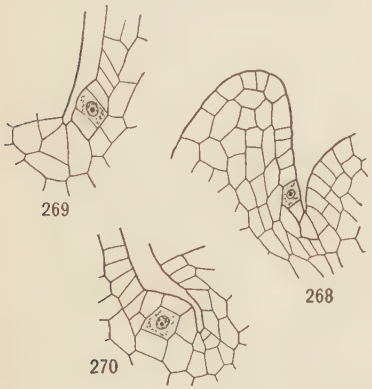


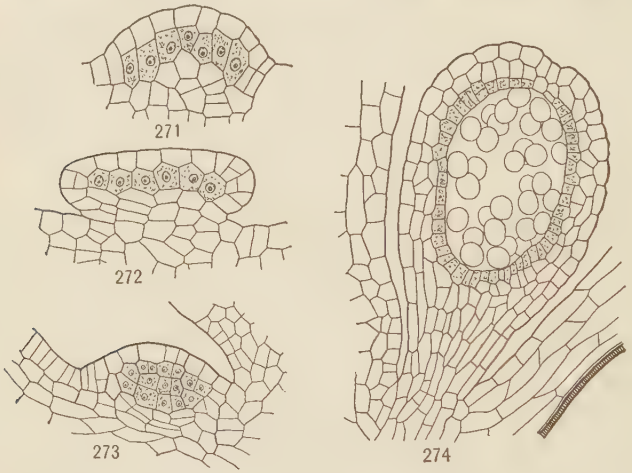
FIG. 267. — Cross section of the central region of an adult stem of *Lycopodium*, showing the inner region of the cortex surrounding the central stele, in which the branches of the xylem mass are irregularly distributed; section of four leaf traces are seen in the cortex, each of them showing the simple concentric arrangement (xylem surrounded by phloem).



FIGS. 268–270. — Sporangium of *Lycopodium:* 268, section showing a young sporophyll bearing a superficial initial cell (one of a transverse row) on its adaxial face near the base; 269, further development of the initial; 270, division of initial into primary wall cell (outer) and primary sporogenous cell (inner). — After BOWER.

Sporangium. — The large sporangium is borne upon the upper (*adaxial*) surface of the sporophyll, near the base. The sporangium initial is superficial (fig. 268), and is a transverse row of six to twelve cells; in some cases it consists of two or three such rows. Each of these initial cells divides by a periclinal wall (parallel with the surface), resulting in an outer and an inner transverse row of cells (figs.

270, 271, 272). The outer cells are the *primary wall cells*, which by subsequent divisions give rise to a sporangium wall of at least three layers of cells. The inner cells are the *primary sporogenous cells*, which by subsequent divisions give rise to a considerable mass of sporogenous tissue (fig. 273). This method of sporangium formation, by which the inner cells, following periclinal division of the superficial initials, give rise to the sporogenous tissue, is called the *eusporangiate* method, and plants exhibiting it are often spoken of as *eusporangiates*. All vascular



FIGS. 271–274. — Sporangium of *Lycopodium:* 271, 272, view of young sporangium in different planes, showing primary wall layer, primary sporogenous tissue (shaded), and the underlying subarchesporial pad; 273, section showing further development of sporogenous tissue; 274, older sporangium, showing stalklike subarchesporial pad, three wall layers, the innermost of which is the tapetum (shaded), and the rounded off and separated spore mother cells. — After BOWER.

plants are eusporangiates except the modern ferns, whose peculiar method of sporangium formation will be described later.

The sporogenous tissue is invested by a special nutritive layer known as the *tapetum* or *tapetal layer* (fig. 274). In *Lycopodium* the outer portion of the tapetal layer is composed of the innermost wall layer, and the inner portion of the sterile tissue contiguous to the sporogenous tissue. The tapetum, therefore, is simply the layer of sterile cells abutting against the sporogenous tissue, which have been transformed into feeding cells. This function gives to the layer a very characteristic appearance, making it quite distinct from the sterile tissue outside

and the sporogenous tissue inside. When the tapetal layer has become a complete investment, the sporogenous cells cease dividing by ordinary division and become *mother cells*, each of which forms a tetrad of spores by two successive divisions, known as the reduction divisions (see p. 61).

Beneath the sporangium, which in section is often somewhat kidney-shaped, there is developed a cushion of sterile cells or even a short stalk, known as the *subarchesporial pad* (figs. 271, 272, 274), in which the vascular elements end. In certain extinct lycopods with very large sporangia, sterile strands or plates radiate from this subarchesporial pad into the large mass of sporogenous tissue, probably being sterilized sporogenous cells. These sterile strands are important to note, as indicating a tendency to divide a large sporangium into chambers.

Gametophyte. — The gametophyte of *Lycopodium* is a very characteristic structure and suggests very little connection with the gametophytes of liverworts. In what is regarded as the primitive form the spore produces at first a subterranean tuberous body (*primary tubercle*), which later gives rise to an aerial, lobed, green portion (*crown*) bearing the sex organs. The gametophyte is differentiated, therefore, into two distinct regions. The subterranean tuberous part is variable in form and is often highly differentiated into tissue regions (fig. 276); it always contains a characteristic endophytic fungus, which inhabits a definite region of the body. In certain species, however, the crown becomes reduced, is no longer aerial, and therefore not green (fig. 275); while in still others it is not developed at all (fig. 277), the gametophyte being simply a subterranean tuberous body bearing the sex organs. In certain epiphytic species the tuberous region is lacking, the gametophyte being entirely aerial, but not always green.

FIG. 275. Gametophyte of *Lycopodium complanatum*, showing the differentiation into tuberous region and crown. — After BRUCHMANN.

Antheridium. — The antheridium (figs. 278–282) begins as a superficial cell, which enlarges and then divides by a periclinal wall. The outer cell following this division is the *primary wall cell*, which forms an outer wall of one layer of cells; the inner cell is the *primary spermatogenous cell*, which produces a large number of spermatogenous cells, those of the last division being sperm mother cells. This method of

antheridium development resembles closely the eusporangiate method of sporangium development, and is always associated with it. It is interesting to note that only the Anthocerotales among bryophytes approach this method of antheridium formation in the fact that the inner cell following the periclinal division gives rise to the spermatogenous tissue. The sperms are remarkable among pteridophytes in being biciliate, a character which belongs to the sperms of bryophytes (fig. 282).

FIG. 276. — Section of gametophyte of *Lycopodium complanatum*, showing crown (*g*) bearing antheridia (*a*) and archegonia (*a'*) (in one, *e*, the embryo sporophyte has developed), and the tuberous region (*c*) with highly differentiated tissues. — After BRUCHMANN.

Archegonium.— The archegonium also resembles that of the Anthocerotales in being an embedded structure. The outline of its development is as follows: It begins as a superficial cell, which divides by a transverse wall (fig. 283), the outer cell being the *primary neck cell*, the inner one the *inner cell*. The inner cell divides by a transverse wall, resulting in a row of three cells (fig. 284), a condition of the archegonium very commonly seen. Beginning with the

outermost one of this row of cells, they are called *primary neck cell*, *central cell*, and *basal cell*. The primary neck cell, by successive divisions, develops a neck consisting of several tiers of cells (figs. 284–286), with four cells in each tier. The central cell develops the axial row as follows: the first transverse division results in the *primary neck canal cell* (the outer one) and the *primary ventral cell* (the inner one, fig. 285). By successive transverse divisions, the primary neck canal cell produces a variable

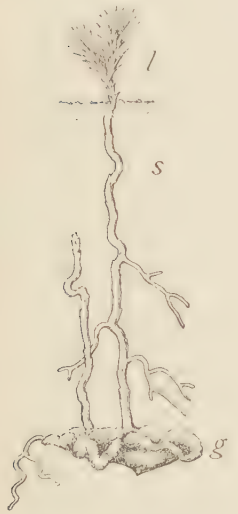
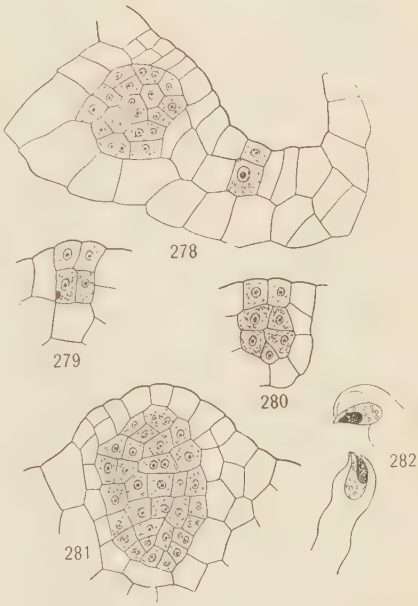


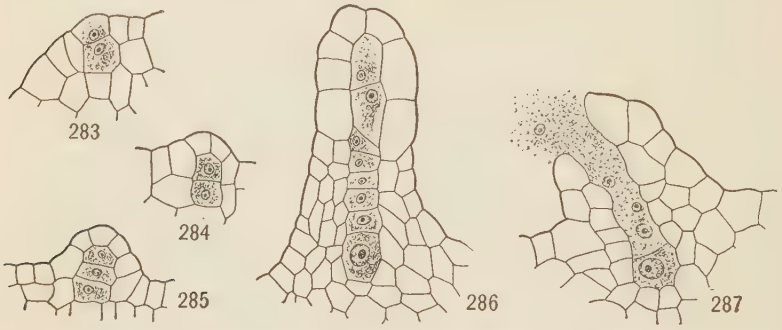
FIG. 277. — Gametophyte (*g*) of *Lycopodium annotinum* (entirely tuberous and subterranean), bearing a young sporophyte (*s*, *l*); the ground line is shown. — After BRUCHMANN.



FIGS. 278–282. — Antheridium of *Lycopodium clavatum:* 278, to the right a young antheridium after the first division (periclinal) of the superficial initial cell; to the left a much older antheridium; 279, young antheridium after division of primary wall cell and primary spermatogenous cell; 280, further development of spermatogenous tissue; 281, nearly mature antheridium, showing the wall (consisting of one layer of cells) and the mass of spermatogenous cells; 282, two sperms, showing the biciliate character. — After BRUCHMANN.

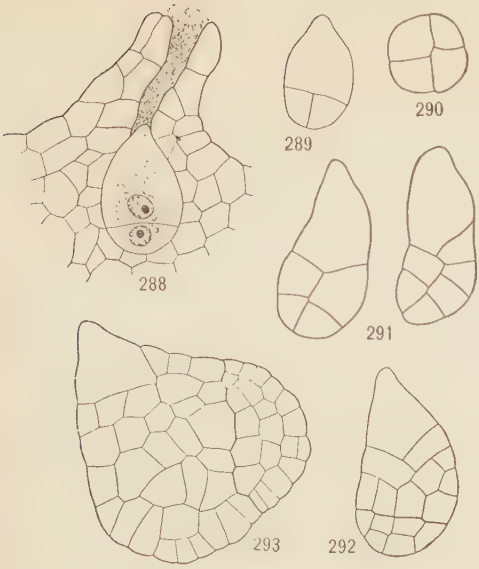
number of neck canal cells (fig. 286) ; in some cases four to six, but in other cases as many as thirteen have been observed. This extraordinarily large number of neck canal cells is regarded as a low character, since a steady decrease in the number of neck canal cells

is observed throughout the groups having archegonia. The primary ventral cell, just before the maturity of the archegonium, divides into the ventral canal cell and the egg, and finally all the canal cells disorganize (fig. 287).



FIGS. 283–287. — Archegonium of *Lycopodium clavatum:* 283, young archegonium after the first division (periclinal) of the superficial initial, resulting in the primary neck cell (outer) and inner cell; 284, division of neck cell and also of inner cell, the latter division resulting in basal cell and central cell (both shaded); 285, division of central cell, giving rise to primary neck canal cell (outermost shaded one) and primary ventral cell (middle shaded one); 286, the completed axial row, consisting of six neck canal cells, the ventral canal cell, and the egg; 287, breaking down of canal cells, leaving a passageway to the egg. — After BRUCHMANN.

Embryo. — The embryo of the *Lycopodium* sporophyte develops in a very characteristic way (figs. 288–293). The fertilized egg divides by a transverse wall, the resulting outer cell being the *suspensor cell*, and the inner one the *embryonal cell* (fig. 288). The suspensor cell may or may not divide, but in any event it usually becomes elongated. The suspensor is an organ of the embryo, but does not enter into its permanent structure, which is developed by the embryonal cell. By successive divisions this cell becomes four cells (figs. 289, 290), which are related to each other as unequal quadrants of a sphere. Two of these quadrant cells develop the *foot*, which is an absorbing organ of the embryo while it is feeding upon the gametophyte. One of the remaining quadrant cells develops the stem, and the other the first leaf. It is to be observed that in this first differentiation of body regions the root is omitted, but it develops later from the tissue produced by the leaf quadrant (fig. 294). The foot is a structure of the sporophyte found among the bryophytes, among which the sporophyte is dependent on the gametophyte through life. The suspensor is a new organ of the



FIGS. 288–293. — Embryo (sporophyte) of *Lycopodium clavatum:* 288, first division of egg into suspensor cell and embryonal cell; 289, 290, division of embryonal cell into four cells (290 being a cross section); 291–293, further stages in the development of the embryo. — After BRUCHMANN.

FIG. 294. — Young sporophyte of *Lycopodium clavatum*, showing foot, primary root, and stem bearing scale leaves. — After BRUCHMANN.

embryo sporophyte, found in certain pteridophytes, as the Lycopodiales, but very characteristic of seed plants

Phylloglossum

This is an Australasian genus of one species, closely allied to *Lycopodium* and thought by some to be the most primitive pteridophyte. The sporophyte body is a tuberous stem bearing a cluster of small leaves. Some of the sporophytes also develop a short, naked stalk bearing a terminal stobilus (fig. 295). Some species of *Lycopodium* begin with this type of body, but the strobilus-bearing stalk becomes branching and leafy, and the tuberous embryonic body disappears. The adult body of *Phylloglossum*, therefore, is like the embryonic body of some species of *Lycopodium*. In other species of *Lycopodium* this kind of embryonic body is absent from the life history. The gametophyte resembles that of *Lycopodium*, in which there is a subterranean

tuberous region and an aerial, green, more or less lobed region bearing the sex organs.

Conclusions. — Since *Lycopodium* and its ally represent possibly the most primitive vascular plants, a summary of the important features will be useful. It would follow that the most primitive leafy sporophyte is a strobilus, in the sense that all its leaves are sporophylls. The first foliage leaves are small and scattered, and are sterilized sporophylls. The vascular system consists of a single, solid cylinder, whose xylem and phloem are concentrically arranged. The sporangia are large and solitary on the adaxial face of the sporophyll, and each one is developed from a transverse row of initial cells. The new structures of this sporophyte, as contrasted with that of the bryophytes, are sporophylls, foliage leaves, vascular system, root, and suspensor.

FIG. 295. — *Phylloglossum:* sporophyte bearing a stalked strobilus.

The gametophyte is a subterranean tuberous body with an aerial, green crown bearing the sex organs. The antheridia develop endogenously, and the sperms are bryophytic in type. The archegonia are also embedded, as in Anthocerotales.

Selaginella

General character. — This is the great genus of modern Lycopodiales, comprising nearly 500 species, which belong chiefly to the tropics. It is evidently closely related to *Lycopodium*, and may be regarded as a modern representative of forms that lived during the coal measures, and that had developed *heterospory* (see below).

Sporophyte. — The sporophyte body resembles that of *Lycopodium* in habit (fig. 296), although it is usually much more delicate. It is characterized by two noteworthy features. One is the development of a *ligule*, a flaplike outgrowth from the adaxial surface of the leaf near its base. The ligule is an embryonic organ of the leaf, being very prominent and functional during the growth of the leaf blade. When the blade matures, the ligule becomes merely an inconspicuous and membranous flap. This curious structure is a feature of all the Lycopodiales (including fossil groups) except *Lycopodium* and *Phylloglossum*, and for this reason the former are often called *Ligulatae*, to distinguish them from the latter, which are *Eligulatae*. The other

noteworthy feature of the sporophyte body is the occurrence of a single chloroplast in the actively dividing cells (*meristem*). It will be remembered that this same feature appears in the gametophyte body of *Anthoceros* (p. 106).

The vascular cylinder of the stem is generally of the primitive type, being a protostele (p. 125) (fig. 297); but in some cases the cylinder is hollow (a *siphonostele*), containing pith, a type of cylinder derived from the protostele.

FIG. 296. — *Selaginella:* sporophyte showing strobili and the gradation from foliage leaves to sporophylls.

Sporangia. — The sporangia, as in all Lycopodiales, are solitary and adaxial with reference to the sporophyll, and derived from a transverse row of initial cells; but in *Selaginella* these initials occur on the stem just above the origin of the sporophyll (figs. 298, 299). This means that sporangia are not always produced by sporophylls, and in such cases the name sporophyll is justified only by its relation to the sporangium. On the basis of their origin, sporangia often are distinguished as *foliar* (on the sporophyll) and *cauline* (on the stem).

Heterospory. — The notable feature of *Selaginella*, however, is that all of the sporangia in a strobilus do not mature alike, resulting in heterospory. They all develop alike, and as described under *Lycopodium* (p. 125), as far as the mother cell stage (fig. 300), after which a great difference appears. In some of the sporangia (usually the larger number) all or nearly all of the mother cells function, resulting in the production of numerous spores (fig. 301). In the other sporangia an extensive abortion of mother cells occurs, so

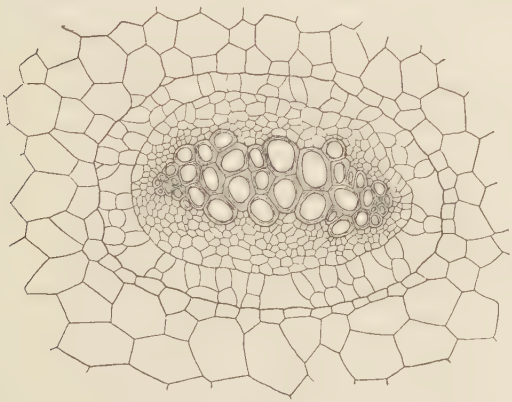
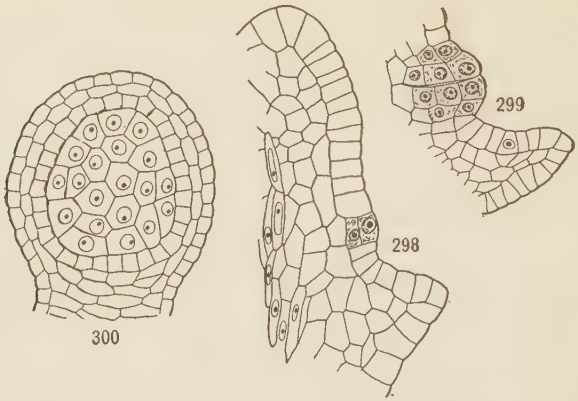


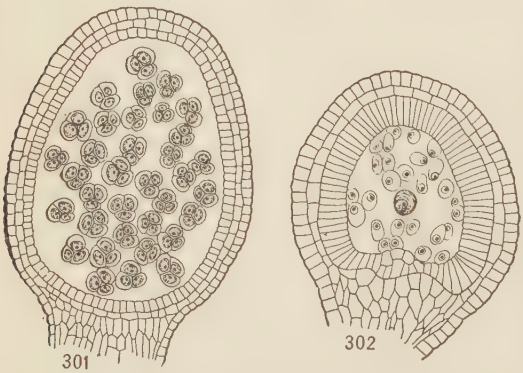
FIG. 297. — Section of stem of *Selaginella*, showing the protostele (a single, solid, concentric vascular cylinder).

extensive that usually only one mother cell functions, all the others contributing to its nutrition (fig. 302). This results in a relatively very



FIGS. 298–300. — Sporangium of *Selaginella:* 298, section through tip of strobilus, showing young sporangium (two shaded cells) on stem, and below it a young sporophyll; 299, further development of sporangium; the superficial cell of the sporophyll containing a nucleus is to give rise to the ligule; 300, sporangium in the mother cell stage. — 298 and 299, after MISS LYON.

large mother cell and a tetrad of four very large spores. In some cases, although a tetrad of spores is started, two or three of them may not develop further, resulting in a sporangium containing only one or two spores. It is this condition of dissimilar spores that is called *heterospory*, in contrast with the condition of similar spores (as in *Lycopodium*), which is called *homospory*. *Selaginella*, therefore, is *heterosporous*, while *Lycopodium* is *homosporous*.



FIGS. 301, 302. — Sporangia of *Selaginella:* 301, microsporangium, showing all the mother cells forming tetrads; 302, megasporangium, showing one functioning mother cell (shaded), the other mother cells acting as nutritive cells. — After MISS LYON.

The terminology applied to the heterosporous condition is simple. The small

spores are *microspores*, and the large ones are *megaspores;* the sporangia producing microspores are *microsporangia*, and those producing megaspores are *megasporangia;* the sporophylls related to microsporangia are *microsporophylls*, and those related to megasporangia are *megasporophylls*.

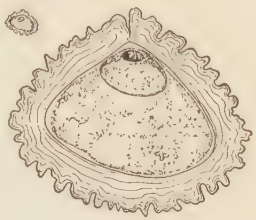
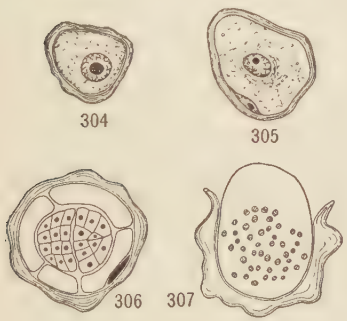


FIG. 303. — Spores of *Selaginella:* mature microspore and megaspore drawn to same scale.

This differentiation of spores in size (fig. 303) is associated with a differentiation in function, for upon germination the microspores produce male gametophytes, while the megaspores produce female gametophytes. The phenomenon of heterospory, therefore, is associated with the sexual differentiation of gametophytes. It is a phenomenon exhibited among pteridophytes only by certain groups, but it is universal among seed plants. In fact, the appearance of heterospory is the necessary antecedent to the formation of a seed. It follows, therefore, that the development of heterospory among pteridophytes made the great group of seed plants possible. In *Selaginella* there is a remarkable approach to the seed condition in the fact that the megaspores are not shed, but are retained within the megasporangium, within which the female gametophyte is developed, the egg fertilized, and the young sporophyte (embryo) formed. Just how far this falls short of being the seed condition will be considered under seed plants.



FIGS. 304–307. — Male gametophyte of *Selaginella:* 304, mature microspore; 305, first division, showing antheridium initial (large cell) and vegetative cell (small lenticular cell against the wall); 306, the antheridium (four sterile jacket cells shown surrounding the group of sperm mother cells); the disorganized vegetative cell is also shown (in black); 307, male gametophyte at time of fertilization, the antheridium (jacket cells have broken down) containing free sperms escaping from the microspore wall. — After MISS LYON.

Male gametophyte. — The male gametophyte produced by the microspore is a very simple structure, never outgrowing the spore, and therefore encased by the old spore wall. The two cells formed by the division of the protoplast of the microspore are the antheridium initial and the vegetative cell (fig. 305). This single vegetative cell is the sole representative of the

vegetative tissue of more primitive gametophytes. The antheridium initial produces an antheridium with the usual jacket of sterile cells investing sperm mother cells (fig. 306). At maturity the jacket cells break down and the mother cells (with their sperms) are free in the general cavity of the microspore (fig. 307). The male gametophyte, therefore, is reduced to one vegetative cell and one antheridium; and encased by the old microspore wall it is carried to the megasporangium, in which the female gametophytes are developing. There the male gametophyte bursts through the microspore coat (fig. 307). The sperms are very small, with more or less spirally coiled bodies and two terminal cilia. *Selaginella* thus shares with *Lycopodium* and *Phylloglossum* the character of producing biciliate sperms, a type characteristic of bryophytes, and in strong contrast with the sperms produced by other pteridophytes.

Female gametophyte. — The female gametophyte is much more extensive than the male gametophyte, but the greater part of it is invested by the old megaspore wall (fig. 308). The nucleus of the megaspore begins a series of divisions that continue until a large number of free nuclei are produced. This free nuclear division occurs chiefly in the apical (pointed) end of the megaspore, and results in a layer of nuclei, which later become invested by walls. Subsequent divisions result in a cushion of cells at the apex of the megaspore, while the large body of the megaspore is free from cells, acting as a great food reservoir (fig. 308). The wall of the megaspore cracks at the apex and the apical tissue protrudes, developing a more or less expanded mass of tissue in which archegonia develop (figs. 308, 309). Later, the deeper region of the megaspore becomes filled with a tissue of large cells, and continues to act as a food reservoir for the developing embryo. This early differentiation of the female gametophyte into two distinct regions, one that produces archegonia, and the other nutritive, is a marked feature of the female gametophyte in all heterosporous plants.

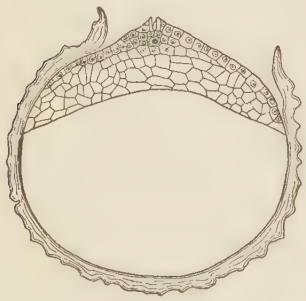
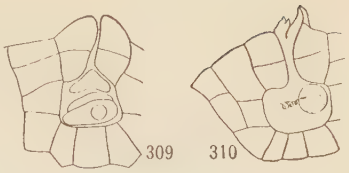


FIG. 308. — Female gametophyte of *Selaginella:* the apical cushion of cells having broken through the heavy megaspore wall; an archegonium to be observed at the apex. — After MISS LYON.

Fertilization. — The male gametophytes enclosed by the old micro-

spore walls are brought to the megasporangia by the wind or by gravity. The microspores drift among the megaspores with protruding female gametophytes bearing archegonia. Then the sperms are discharged, enter the archegonia, and fertilization occurs (fig. 310). In these female gametophytes, still in the sporangia, the embryo sporophytes develop and then emerge, a strobilus often being beset with young sporelings. Later the strobilus as a whole, with its attached sporelings, drops off.



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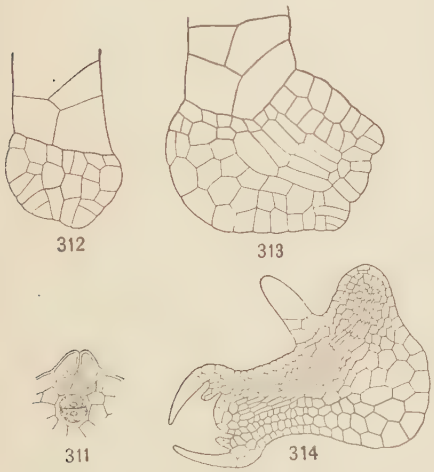
FIGS. 309, 310. — Archegonium of *Selaginella:* 309, the neck and the axial row (neck canal cell, ventral canal cell, and egg); 310, fertilization, the sperm in contact with the egg. — After MISS LYON.

Embryo. — The embryo (sporophyte) is developed much as in *Lycopodium* (figs. 311–314). The suspensor (p. 130) is more extensive than in *Lycopodium*, being of use in relating the embryo to the deep nutritive tissue within the megaspore. The embryonal cell at the end of the suspensor first produces three cells: a terminal cell that develops the stem, flanked by two cells (one on each side) that develop leaves. From one of the leaf segments the foot is developed later (fig. 313); and still later, from the same segment the primary root arises (fig. 314). When fully organized and emerging, the embryo resembles a seedling dicotyledon escaping from its seed. The tuberous foot



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311 314

FIGS. 311–314. — Embryo of *Selaginella:* 311, first division of fertilized egg (the outer cell to form the suspensor, the inner cell to form the embryo); 312, early stage of the embryo (attached to suspensor), the apical cell of the stem being evident; 313, later stage of the embryo, showing (to the right) the apical cell of the stem between the apical cells of the first two leaves and (to the left) the developing foot; 314, an older embryo, showing the foot (to the right below), the root (to the right above), the suspensor, the two leaves (to the left) with their ligules, the centrally placed stem tip, and the developing vascular system extending between stem and root tips — 311, after BRUCHMANN; 312–314, after PFEFFER.

FIG. 315. — *Isoetes*, showing the short unbranched stem bearing dichotomous roots and a tuft of linear leaves.

is embedded in the nutritive region of the female gametophyte invested by the megaspore coat, and from it there extends in one direction, outside of the spore coat, an elongating stem bearing at its tip a pair of young leaves, between which is the stem apex; and in the other direction the elongating primary root (fig. 314).

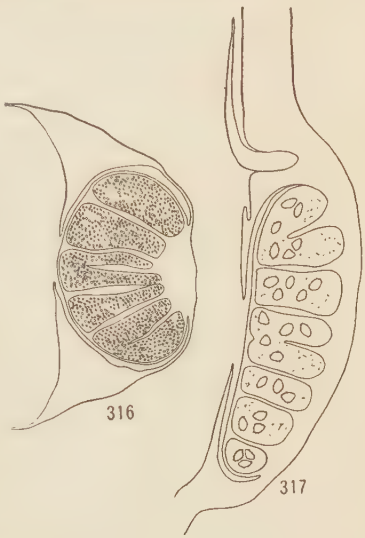
Isoetes

General character. — The genus *Isoetes* (quillworts) comprises about sixty species. It is now usually included among the Lycopodiales, although in certain important features it differs from the other members of the group.

Sporophyte. — In general appearance *Isoetes* suggests a tufted grass, growing on muddy flats or in the water (fig. 315). The stem is very short, unbranched, and covered by overlapping leaf bases. The vascular anatomy of the stem is somewhat confusing, and has been interpreted variously. The stem is so short and the leaves are so numerous that the vascular cylinder is little more than a vascular plate. It seems to be a protostele, however, in which the xylem elements have not completely filled up their region, and there is no recognizable phloem. Such a structure is evidently related to that found among the Lycopodiales, and therefore in vascular anatomy *Isoetes* is to be associated with that group.

Leaves. — The leaves are unique in structure, being arranged in a close-

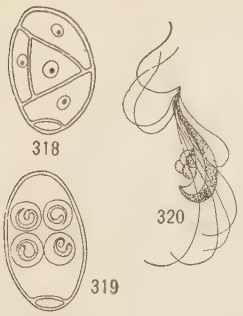
spiral, and every leaf is a sporophyll, either bearing a sporangium or traces of one. In this sense the whole sporophyte body is a strobilus. Each leaf is distinctly differentiated into sporangium and foliage regions (fig. 317). The foliage portion of the leaf resembles a narrow grass blade, and contains four longitudinal series of air chambers. At the base of this blade, on the adaxial side, the *ligule* appears, socketed in a small pitlike depression. Below the ligule the sporangium region occurs, the sporangium developing in a large deep chamber more or less shut off from the outside by a curtain of tissue (*velum*). This single large sporangium on the adaxial surface of the sporophyll is a very important character relating *Isoetes* to the other Lycopodiales.



FIGS. 316, 317. — Sporangia of *Isoetes:* 316, cross section of lower region of leaf, showing a microsporangium, with its trabeculae (sterile plates) and numerous microspores; 317, longitudinal section of lower region of leaf, showing a megasporangium, with its trabeculae and relatively few megaspores; also the ligule (above) and the velum extending over the sporangial chamber.

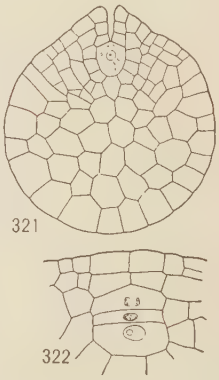
Sporangia. — The sporangium resembles also that of the Lycopodiales in arising from a transverse row of initial cells, in this case three or four in number. The method of development is as usual in eusporangiates, beginning with a periclinal division that differentiates the outer wall cells from the inner sporogenous cells. The wall becomes about four-layered, the innermost layer entering into the organization of the tapetal jacket. A large mass of sporogenous tissue is developed, and up to 15,000–25,000 cells all sporangia are alike. At this stage the differences that result in heterospory begin to appear. In those sporangia that are to become microsporangia some of the sporogenous tissue forms plates of sterile cells (*trabeculae*) extending across the sporangium, and all the other cells function in spore formation, producing in a single sporangium 150,000–300,000 microspores (fig. 316). In those sporangia that are to become megasporangia, the trabeculae are more massive, and most of the thousands of sporogenous

cells contribute to the nutrition of 40–75 mother cells that function. These mother cells become relatively very large and produce large spores, the total output of megaspores being 150–300 (fig. 317). Both kinds of spores escape by the decay of the sporangium wall.



FIGS. 318–320. — Male gametophyte of *Isoëtes:* 318, stage showing the vegetative cell (at bottom and without nucleus) and the antheridium (with three wall cells visible and the central primary spermatogenous cell); 319, older stage, in which the wall cells have broken down and the four mother cells (each containing a sperm) are free in the antheridial cavity; 320, sperm. — After BELAJEFF.

Male gametophyte. — The male gametophyte is still more simple than that of *Selaginella* (figs. 318–320). It consists of a single vegetative cell and a single antheridium, as in *Selaginella;* but the sperm mother cells are only four in number. This is the lowest number reached among pteridophytes, and the nearest approach to seed plants, among which the sperm mother cells are reduced to two. The sperms are large, spirally coiled, and multiciliate (fig. 320), such as characterize all other pteridophytes except Lycopodiales. It is this feature of *Isoetes* that perhaps presents the greatest obstacle to including it among Lycopodiales.

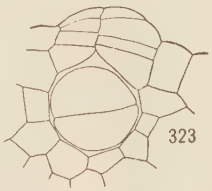


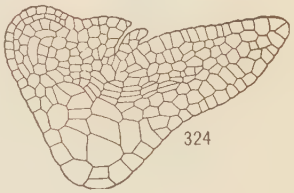
FIGS. 321, 322. — Female gametophyte of *Isoetes:* 321 (after HOFMEISTER), complete gametophyte, bearing an archegonium whose neck is exposed through a crack in the megaspore wall (not shown); 322 (after CAMPBELL), archegonium, showing two tiers of neck cells and an axial row of three cells (neck canal cell, ventral canal cell, and egg).

Female gametophyte. — The female gametophyte develops in the same general way as does that of *Selaginella*, but with some interesting differences. After the free nuclear divisions, followed by the formation of an apical tissue, a layer of cells develops completely about the cavity of the megaspore and then grows centripetally until the megaspore is filled with tissue (fig. 321). The growth of this tissue is precisely like the growth of the endosperm tissue (female gametophyte) in gymnosperms (p. 196). The gametophyte of *Isoetes* does not protrude through the broken megaspore wall and develop tissue outside, as in *Selaginella*, but is exposed only

along the triradiate crack through the megaspore wall, along which lines the archegonia appear (fig. 322). The archegonium is notably broad and short, and the primary neck canal cell usually does not divide, resulting in a single uninucleate neck canal cell, which is as far as the reduction of the axial row is carried among pteridophytes (fig. 322).

Embryo. — The embryo sporophyte differs from that of *Selaginella* and *Lycopodium* in several important particulars. In the first place, there is no suspensor, and this feature associates *Isoetes* with the other pteridophytes. The fertilized egg, however, behaves much as does the embryonal cell in *Selaginella* and *Lycopodium*, except that the quadrant cells are assigned differently, two of them forming the foot (as in *Lycopodium*), and the other two forming leaf and root, the stem being the belated member. However, it is characteristic of Lycopodiales to have some member of the body belated in appearance. In *Lycopodium* the belated member is the root, in *Selaginella* the foot and root, in *Isoetes* the stem. The embryo of *Isoetes* has long been recognized to have a remarkable resemblance to the characteristic embryo of monocotyledons among seed plants; and for this reason it was once suggested that perhaps *Isoetes* is a living representative of the ancestors of monocotyledons. In *Isoetes* the axis of the embryo develops the root at one end and a single leaf (*cotyledon*) at the other, the foot arising from the middle region and being embedded in the nutritive tissue within the megaspore. On the free side of the axis a notch appears, from the bottom of which the stem tip arises (fig. 324). The feature of the embryo of monocotyledons is that the single cotyledon is terminal and the stem tip is lateral, and this feature is exactly reproduced in the embryo of *Isoetes*.





FIGS. 323, 324. — Embryo of *Isoetes*: 323, first division of the fertilized egg, differing from that of *Selaginella* in that the outer (upper) cell does not form a suspensor, but enters into the structure of the embryo; 324, embryo showing foot (below), terminal cotyledon (to the right), root (to the left), ligule (above) from deep notch, and shallow notch (between ligule and root) for stem tip. — After CAMPBELL.

Summary. — A summary of the arguments for and against retaining *Isoetes* among Lycopodiales is as follows: its characters in common

with Lycopodiales are (1) the vascular anatomy; (2) the solitary sporangium on the adaxial surface of the sporophyll; (3) the development of the sporangium from a transverse row of initial cells; (4) the trabeculae, which also appear in certain fossil Lycopodiales; (5) the ligule, which is present in all Lycopodiales except *Lycopodium* and *Phylloglossum;* and (6) the gametophytes, which resemble closely those of *Selaginella.* The characters not in common with Lycopodiales are (1) the large multiciliate sperms; (2) the absence of a suspensor; (3) the general habit; and (4) the highly specialized leaves.

FIGS. 325–328. — *Tmesipteris:* 325, general habit, showing branching leafy stems arising from a tree trunk (epiphytic) and bearing (near tip) the characteristic sporangia; 326–328, various views of the paired sporangia (synangia). — After PRITZEL (ENGLER and PRANTL).

(2) PSILOTALES

This group of pteridophytes comprises two very small living genera: *Psilotum* (fig. 330), with two species occurring in the tropics of both hemispheres; and *Tmesipteris* (fig. 325), with a single Australasian species (sometimes more species are recognized). These forms are introduced here, not to present their life histories, but to illustrate very briefly certain stages in the evolution of pteridophytes.

FIG. 329. — *Tmesipteris:* section of sporangia at early stage, showing between the two sporogenous masses a sterile plate of cells which is to form the partition that divides a sporangium (single at the beginning) into two sporangia. — After BOWER.

Throughout Lycopodiales there appears a tendency to increase the output of spores produced by the sporophyte. The first and simplest method was by branching, thus multiplying strobili. There was also an increase in the size of sporangia; and this led, apparently for nutritive reasons, to the development of sterilized plates through the sporangium, as in certain ancient lycopods; and in *Isoetes* these plates almost divide the sporangium into chambers.

In *Psilotum* and *Tmesipteris* there are two further stages of development in this

direction. In *Tmesipteris* a sterile plate divides the large sporangium into two chambers so distinct that they are called two sporangia (figs. 326–329). That this partition is sterilized sporogenous tissue is proved by its development and by the fact that in exceptional cases it functions as sporogenous tissue. In *Psilotum* the same condition occurs, except that the development of two sterile plates results in three chambers, or a group of three sporangia (figs. 330, 331). The other noteworthy feature of *Psilotum* and *Tmesipteris* is the development of the subarchesporial pad of Lycopodiales into a short stalk, which bears the two or three sporangia and is called the ***sporangiophore.***

(3) Sphenophyllales

This group contains the single large Carboniferous genus *Sphenophyllum*, which illustrates the further development of the sporangiophore. In *Sphenophyllum* there is a distinct strobilus, with whorls of linear sporophylls coalescent at base into spreading funnels. From the adaxial surface of these sporophylls sporangiophores arise, which vary from very short to very long, simple or branching, and bear one to several sporangia. In this genus, therefore, the sporangiophore development is carried much farther than in *Psilotum* and *Tmesipteris*, resulting in a multiplication of sporangia by means of the sporangiophore.

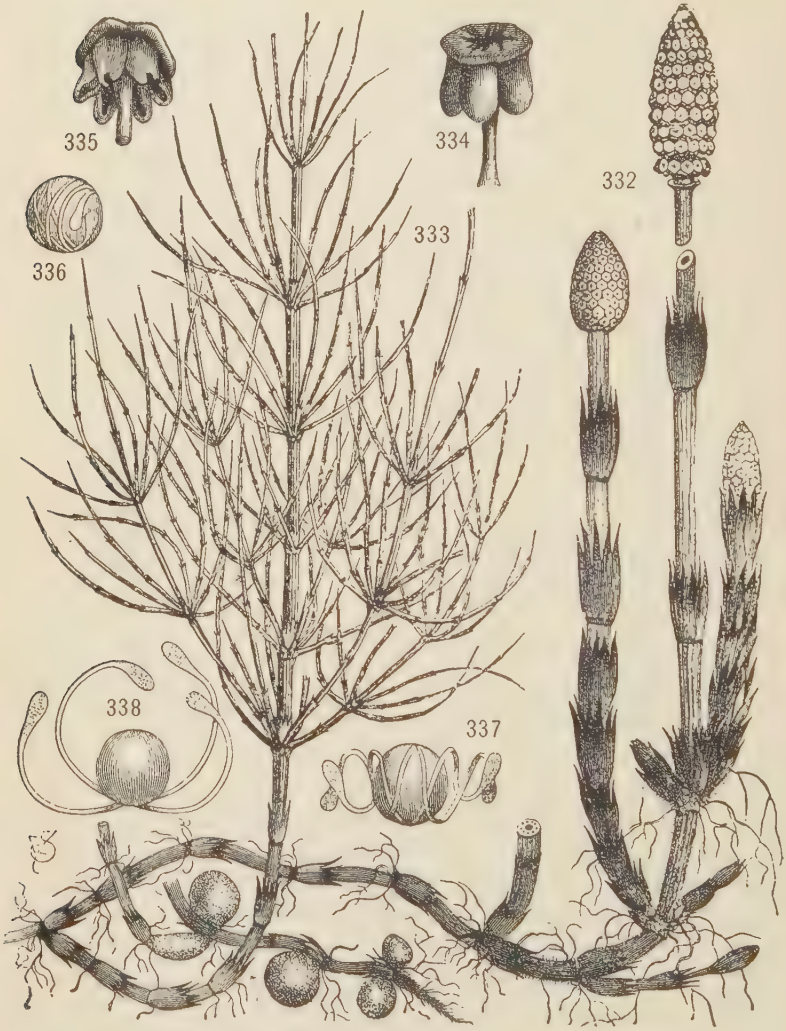
(4) Equisetales

This great group is represented in our present flora by the single genus *Equisetum*, comprising about twenty-five species of horsetails or scouring rushes. This is only a remnant of a great group that flourished in the Paleozoic along with the ancient Lycopodiales.

Sporophyte. — The sporophyte body consists of a subterranean, dorsiventral main axis, which gives rise to erect (radial) aerial branches, themselves simple or branched (figs. 332, 333). *Equisetum* is characterized by its remarkably small leaves, which for the most part are insignificant scales that occur in a whorl at each joint and coalesce to form a close sheath. As a conse-

Figs. 330, 331. — *Psilotum:* 330, general habit, showing the branching body bearing much reduced leaves (scales) and the characteristic three-lobed sporangium (or synangium of three sporangia); 331, the sporangia in greater detail.

quence of this abandonment of leaves as foliage, photosynthesis is entirely a function of the green tissue of the stem. Many of the older forms were leafy, but all Equisetales are characterized by the



FIGS. 332–338. — *Equisetum arvense:* 332, fertile branches from the dorsiventral stem, each bearing a terminal strobilus, one of them mature; 333, sterile branch; 334, 335, two views of a sporangiophore (so-called "sporophyll"); 336–338, spores showing the unwinding of the perinium. — After WOSSIDLO.

occurrence of the leaves in cycles (whorls) instead of in the scattered or spiral arrangement observed in the first two groups. In Sphenophyllales the same cyclic arrangement of leaves occurs, and this disposition of the leaves is associated with very distinct differentiation of the stem into *nodes* and *internodes*. Such a differentiation means a localization of the power of producing lateral members, which is not generally distributed, but is restricted to the nodes. It is from the nodes, therefore, that the leaves arise, and from the axils of the leaves that the branches arise. The aerial branches may be all alike, or they may be dimorphic, as in *E. arvense*, in which case special strobilus-bearing branches mature in the spring, and later the green vegetative branches develop (figs. 332, 333).

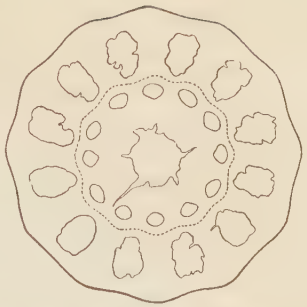


FIG. 339. — Cross section of stem of *Equisetum:* outer zone is cortex containing large air passages (one beneath each furrow); inner region (bounded by dotted line) is the stele, containing a ring (in section) of vascular bundles (one beneath each ridge) enclosing the pith (which is breaking down).

Stem structure. — The structure of the stem is remarkably specialized

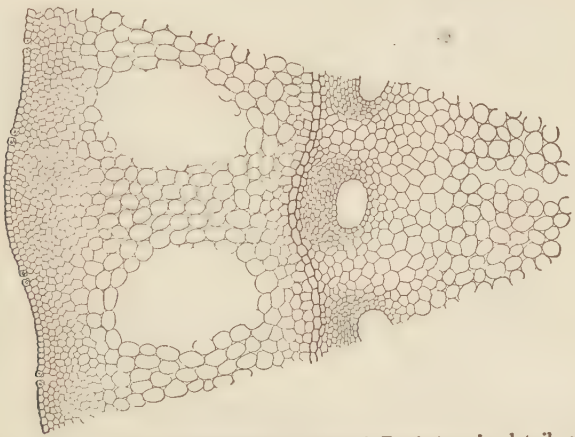
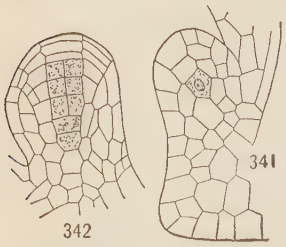


FIG. 340. — Segment of cross section of stem of *Equisetum* in detail, showing epidermis (with stomata), zone of fibrous cells beneath the epidermis, the deeper zone of chlorophyll tissue (penetrating the fibrous zone under the stomata), the large air passages of the cortex, the layer of cortical cells bounding the stele (endodermis), the collateral vascular bundles (each showing phloem, but with xylem replaced by an air passage), and the central pith.

(figs. 339, 340). The outer walls of the epidermal cells are so impregnated by a deposit of silica as to give the characteristic rough feeling to the stem. The stem is fluted, and within the ridges strands of fibrous cells are developed; while in the furrows the chlorophyll tissue reaches the epidermis. It follows that the *stomata* (see p. 250) are in the furrows (usually along the slopes) rather than on the ridges. Deeper within the cortex a zone of large air passages occurs, each one lying beneath a furrow. The central cylinder or stele is remarkably reduced, the vascular bundles being very feebly developed. They are arranged (usually one beneath each ridge) so as to outline a hollow cylinder enclosing a pith, which disappears early; but instead of being concentric bundles, characteristic of most pteridophytes, they are *collateral;* that is, the xylem and phloem strands lie side by side on the same radius, with the xylem towards the center of the stem. In fact, however, in *Equisetum* the xylem is hardly at all developed, its position being occupied by a small air passage (fig. 340).

Sporangium. — The sporangia occur in a very distinct strobilus (fig. 332). The structure usually called a sporophyll has a stalklike base and a peltate top, beneath which five to ten sporangia are borne (figs. 334, 335).

To understand this structure it is necessary to be familiar with certain of the extinct Equisetales. A series can be arranged, beginning with *Sphenophyllum*, passing on to Calamites (an extinct group of Equisetales), and ending with *Equisetum*, which indicates that in the strobilus of *Equisetum* the sporophylls have been suppressed and that the structures bearing sporangia are sporangiophores. In Calamites the strobilus is made up of alternating sets of sporophylls and sporangiophores, and the latter are just such structures as appear in the strobilus of *Equisetum*, without the alternating sets of sporophylls. In *Selaginella* there are sporophylls that do not bear sporangia; and in *Equisetum* there is apparently a strobilus that does not consist of sporophylls.



FIGS. 341, 342. — Sporangium of *Equisetum:* 341, early stage, three cells having arisen from the superficial initial, the innermost (shaded) being sporogenous, the two outer being wall cells; 342, further development of wall layers and sporogenous tissue. — After GOEBEL.

The sporangium arises from a single superficial cell, and not from a transverse row as among Lycopodiales. There is the usual periclinal wall, setting apart an outer wall cell from an inner sporogenous cell, as in all eusporangiates (fig. 341).

Several layers of wall cells are formed, and the innermost wall cells by their division add to the sporogenous tissue (fig. 342). The tapetum investing the sporogenous tissue consists of two or three layers of cells. At least one third of the mother cells do not produce spores, contributing to the nutrition of the remaining two thirds.

Spores. — In the development of the spores a remarkable outermost wall layer is formed. In all ordinary spores the wall develops two layers,

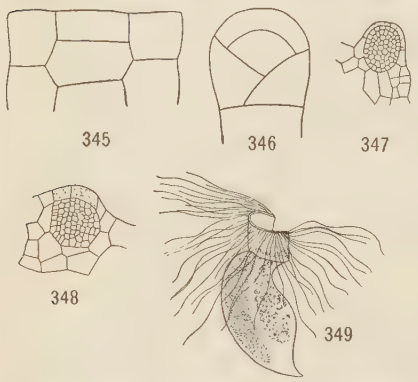
FIGS. 343, 344. — Gametophytes of *Equisetum:* 343, male gametophyte, showing antheridia at some of the branch tips; 344, female gametophyte. — After GOEBEL.

the inner called *intine*, the outer *exine;* but in *Equisetum* another layer is laid down on the exine, called the *perinium*, which cracks into two spirally wound bands that remain connected at one pole of the spore. In shedding, these bands unwind (figs. 336–338), become entangled with the bands of other spores, and thus the spores fall in clumps. This seems to be advantageous since the gametophytes are mostly dioecious;

at least it secures the development of male and female gametophytes in close proximity.

Gametophyte. — The gametophyte is a small, green, branching ribbon, being strictly a thallus, without any of the subterranean development that characterizes *Lycopodium*. Although the gametophytes are usually dioecious, and the female gametophytes are larger and more massive than the male (figs. 343, 344), the spores are all approximately the same size. Certain of the ancient representatives of the Equisetales, however, have been found to be heterosporous.

Antheridium. — The antheridium is interesting in that it shows two kinds of development, dependent upon its position. If it occurs in the axial region of the thallus, it develops as usual among eusporangiates; that is, a superficial initial cell is divided by a periclinal wall, the outer cell producing the wall of the antheridium, the inner cell producing the spermatogenous tissue (figs. 345, 347, 348). If it develops in a terminal position on the thallus, the superficial initial cell forms first a papillate outgrowth, which is cut off by a periclinal wall, and it is this protruding cell that develops the antheridium (fig. 346). In this cell an apical cell with three cutting faces is formed, and then a domelike cap cell is cut off, leaving a central cell, which produces the spermatogenous tissue, invested by four peripheral cells, which develop the wall of the antheridium. This type of antheridium development is characteristic of certain modern ferns. The sperms are very large, spirally coiled, and multiciliate (fig. 349).

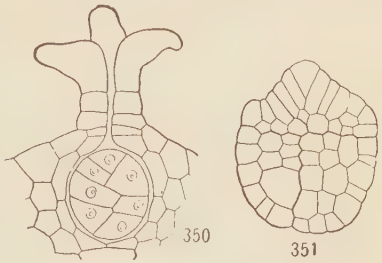


FIGS. 345–349. — Antheridium of *Equisetum*: 345, one type of development, showing the periclinal division, the inner cell being spermatogenous; 346, the other type of development, showing the papillate protruding cell (periclinal wall below), in which are shown two segments (the third behind) cut off by the apical cell, the dome or cap cell, and the enclosed spermatogenous cell; 347, 348, nearly mature antheridia of the first type; 349, a sperm. — 345–348, after GOEBEL; 349, after BELAJEFF.

Archegonium. — The archegonium always develops from the massive axial region and in the axil of a branch. It develops as among other

pteridophytes, but is noteworthy in the fact that its neck canal cells are reduced to two in number.

Embryo. — The development of the embryo differs from that of the Lycopodiales in several particulars. There is no suspensor, and the fertilized egg divides into quadrants, among which all the body regions are distributed; foot and root being developed by the inner quadrants, and stem and leaf by the outer ones (figs. 350, 351). A very heavy calyptra is formed, which is broken through by the vigorous young shoot.



FIGS. 350, 351. — Embryo of *Equisetum*: 350, early stage of embryo, the four body regions having begun to develop; the general structure of the archegonium still evident; 351, more advanced embryo, showing the apical cell that is developing the stem. — After SADEBECK.

Conclusions. — The sporophyte is to be regarded as highly specialized in its leaves, stem anatomy, and strobilus; but its embryogeny appears to be simpler than among Lycopodiales. The gametophyte is entirely aerial; certain antheridia show a specialized form of development; and the archegonia are well advanced, as indicated by the reduction of the neck canal cells.

(5) OPHIOGLOSSALES

General character. — This group of pteridophytes is associated often with Filicales. The three genera usually recognized are *Ophioglossum* (adder's tongue, fig. 352), *Botrychium* (moonwort, fig. 353), and *Helminthostachys* (a New Zealand genus with a single species, fig. 354).[1] The distinguishing character of the group is the so-called fertile spike (a stalk bearing the sporangia), which arises from the adaxial face of the leaf.

Sporophyte. — The sporophyte consists of a subterranean stem covered by the leaf bases, and there are no aerial branches. The leaves are relatively few in number and large, especially in *Botrychium*, and develop very slowly, in some cases becoming aerial only after two or three years of subterranean development. The vascular cylinder is remarkably advanced in structure. It is not only a siphonostele (containing

[1] A fourth genus (*Sceptridium*) has been suggested, including some of the species usually referred to *Botrychium*.

pith), but is made up of collateral bundles (p. 146), separated from one another by *pith rays* (radiating plates of tissue extending from pith to cortex). This is the general structure of the vascular cylinder of the majority of seed plants, and this resemblance is further emphasized

FIG. 352. — General habit of *Ophioglossum*. — After SACHS.

FIG. 353. — General habit of *Botrychium*.

by the presence of a *cambium cylinder* (a meristematic tissue between the xylem and phloem that adds new elements to both). This means increase in diameter by the formation of secondary wood (xylem), and among the elements of this secondary wood there appear *tracheids* with

bordered pits, elements characteristic of gymnosperms (fig. 547), but not of pteridophytes.

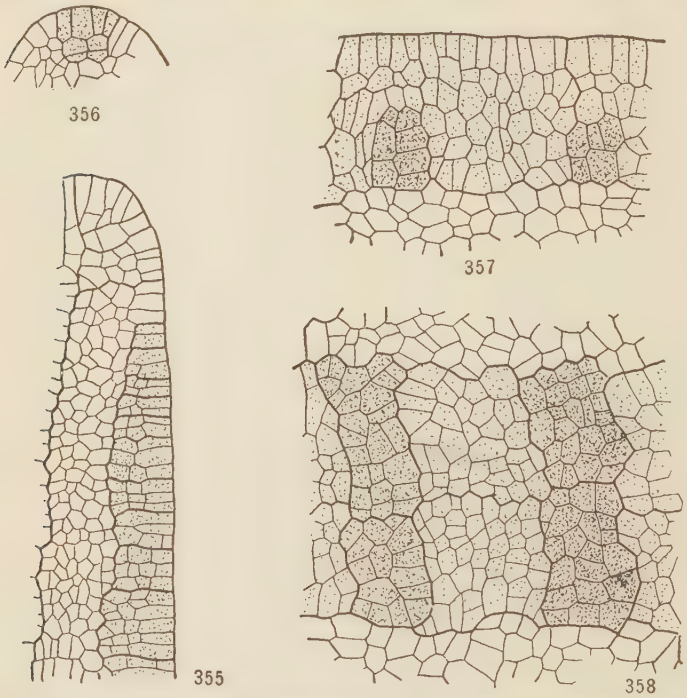
Fertile spike. — In *Ophioglossum* the fertile spike begins to appear very early in the history of the leaf. As it begins to project from the adaxial face of the young leaf, a superficial band of cells becomes differ-

FIG. 354. — General habit of *Helminthostachys*. — After HOOKER.

entiated on each side, from near the apex downwards. As the spike elongates, these two bands elongate and deepen, eventually giving rise to two continuous bands of sporogenous tissue (figs. 355, 356, 359). Later, sterile plates appear across the band, and the individual sporangia become outlined, the single large sporogenous mass being broken up into a great number of sporangia by sterilization (figs. 357, 358).

The situation has suggested the idea that the fertile spike of Ophioglossales is a sporangiophore extremely developed. If this interpretation is true, sporangio-

phore development can be traced from the subarchesporial pad of Lycopodiales to the fertile spike of Ophioglossales, whose leaf would thus become a sporophyll. This conception of the simple spike of *Ophioglossum*, with its sessile sporangia, is difficult to apply to *Helminthostachys* with its stalked sporangia, and to *Botrychium* with its more or less branching spike. Recent anatomical studies, however, suggest that this "fertile spike" may have arisen by the fusion of lateral branches



FIGS. 355–358. — Sporangia of *Ophioglossum:* 355, the band of sporogenous tissue developing on one side of the fertile spike; 356, cross section of the sporogenous band; 357, 358, different stages in sterilization, breaking up the band into separate sporogenous masses, each of which develops a sporangium. — After BOWER.

on opposite sides of the main axis. If this is the case, the relationship with the Marattiaceae and other ferns is clear. It is interesting to note that the spike branches as the leaf branches, being simple in the simple-leaved species of *Ophioglossum* and branching in the compound-leaved species of *Botrychium*.

Sporangium. — The development of the individual sporangium is of the usual eusporangiate type, but the remarkable behavior of the tapetum deserves special mention. The walls of the tapetal cells break down, and the protoplasts thus liberated unite to form a nutritive plas-

modium that grows among the blocks of sporogenous cells and ramifies into every intercellular space (fig. 360).

Gametophyte. — The gametophyte is of the *Lycopodium* type. In *Ophioglossum*, which is regarded as the most primitive genus, the gametophyte is a tuberous, subterranean body that gives rise to aerial green lobes that bear the sex organs. In *Botrychium* there is no aerial portion, the gametophyte being completely subterranean and tuberous (fig. 361). In *Helminthostachys* the gametophyte is somewhat intermediate in structure, the tuberous body giving rise to a cylindrical aerial process that bears the sex organs. In every case the tuberous body contains an endophytic fungus, as in the gametophyte of *Lycopodium*. It is evident that the gametophyte of the Ophioglossales suggests that of the Lycopodiales; but that the sporophyte is more like that of Filicales.

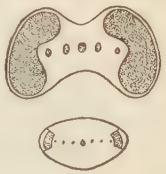


FIG. 359. — Sporangia of *Ophioglossum:* diagrammatic cross section of fertile spike, showing the two sporogenous bands at different stages. — After BOWER.

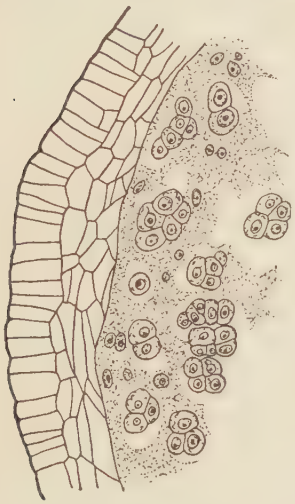


FIG. 360. — Portion of a nearly mature sporangium of *Ophioglossum*, showing the tapetal plasmodium (with nuclei) among the groups of mother cells. — After BOWER.

Sex organs. — The antheridia develop as usual among the eusporangiates, the inner cell, following the periclinal division of the superficial initial, giving rise to the spermatogenous tissue. The sperms are large, coiled, and multiciliate, a type not found among the Lycopodiales, but characteristic of the Filicales.

The archegonium of *Ophioglossum* has a very short neck, the neck canal cells being only two in number, the same reduced number as in *Equisetum*. In *Botrychium* (figs. 362–365) the neck of the archegonium is long, but contains only four neck canal cells.

Embryo. — In general there is no suspensor, but in the recently described genus *Sceptridium* a massive suspensor is reported, at least for one species (formerly *Botrychium obliquum*). There is no differentiation of the great body regions at the quadrant stage, but in *Botrychium*, for example, there is

formed first a rather large, undifferentiated mass of tissue (fig. 365) in which at least three growing points (foot, root, and stem) become organized, the leaf appearing later. In this embryogeny of *Botrychium* there is a general resemblance to the Lycopodiales in the belated organization of some body region; and a still further resemblance to those species of *Lycopodium* in which the embryo begins with the development of a protocorm (p. 131). The same belated appearance of one or more body regions has been observed also in species of *Ophioglossum*. In the whole group there seems to be no such early and complete differentiation of the body regions as in Equisetales and Filicales.

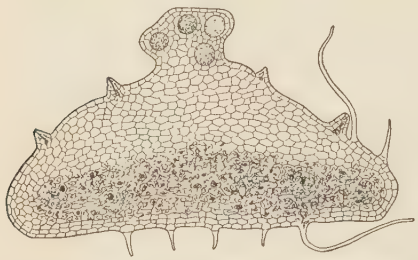
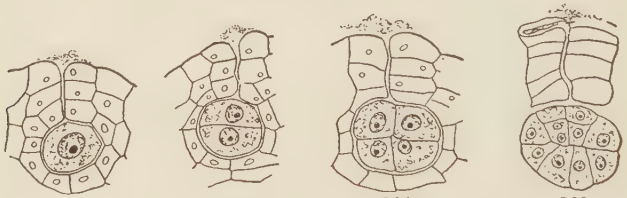


FIG. 361. — Gametophyte of *Botrychium:* antheridia in dorsal ridge; archegonia along the slopes; region of endophytic fungus in ventral region. — After JEFFREY.



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FIGS. 362–365. — Archegonium and embryo of *Botrychium Lunaria:* 362, fertilized egg, in venter of archegonium; 363, first division of egg; 364, quadrant stage; 365, later stage of embryo, the body regions not yet differentiated. — After BRUCHMANN.

Conclusions. — The Ophioglossales have certain features in common with the Lycopodiales, notably the structure of the gametophyte, the adaxial relation of sporangia to sporophylls, and the irregular and somewhat indefinite development of the embryo in its early stages. The "fertile spike," however, may have arisen from lateral branches, which would eliminate this feature of the resemblance to Lycopodiales. The same kind of irregular and indefinite development of the embryo probably also occurs among the Marattiaceae, so that this feature finds its resemblance among both Filicales and Lycopodiales. In the reduced number of foliage leaves and their corresponding increase in size, and in the sperms, the resemblance is decidedly with the Filicales. In vas-

cular structure, the Ophioglossales are more advanced than the majority of pteridophytes. On the whole, the association is evidently with the Filicales of the *Marattia* type.

(6) Filicales

General character. — The ferns constitute by far the largest group of pteridophytes, including at least 3000 living species, and perhaps many more. The group as a whole is very ancient, but most of the living families are very modern. Two groups of Filicales are recognized: *Filicineae* (true ferns), which are homosporous; and *Hydropteridineae* (water ferns), which are heterosporous.

(a) Filicineae

General character. — Nearly all of the living ferns are true ferns. They are well represented throughout the temperate regions, but are especially abundant in the tropics. The sporophyte displays a great variety of habits — ordinary terrestrial forms, epiphytes (perchers), climbers, aquatics, and trees. Ferns are characterized generally by their comparatively few, large, and usually branched leaves, which bear numerous sporangia, usually upon the *abaxial* surface. The multiplication of sporangia is thus facilitated, not by sporangiophore development, but by distribution over a large leaf surface.

Families. — In so large a group it is necessary to have in mind the principal families. Disregarding the smaller families that have been proposed, the following seven may be considered, conveniently but not completely distinguished from one another by the character of the *annulus*. The annulus is a group or band of thick-walled cells developed in the wall of the sporangium and related to its dehiscence.

1. *Marattiaceae* (ringless ferns). — Annulus wanting. About 25 tropical species in 5 genera.

2. *Osmundaceae* (royal ferns). — Annulus rudimentary (fig. 366). About 15 temperate and tropical species in 3 genera.

3. *Gleicheniaceae.* — Annulus equatorial and indusium (see p. 165) wanting (figs. 367, 368). About 25 tropical species in 2 genera.

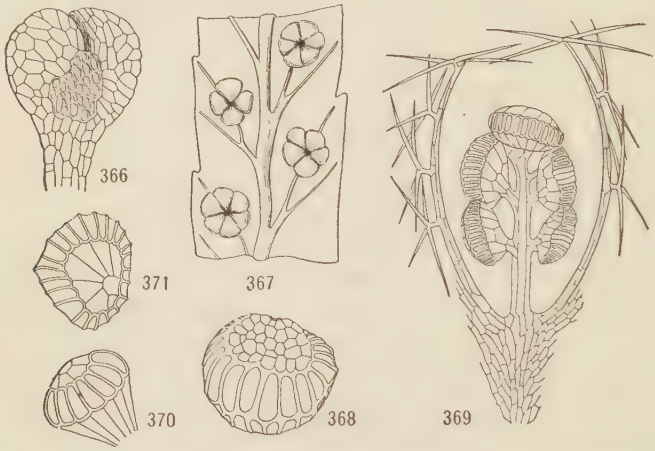
4. *Hymenophyllaceae* (filmy ferns). — Annulus equatorial and indusium present (figs. 369, 370, 371). About 155 species, chiefly tropical, in 2 genera.

5. *Schizaeaceae.* — Annulus apical (figs. 372, 373, 374). About 95 species, chiefly tropical, in 4 genera.

6. *Cyatheaceae* (tree ferns). — Annulus vertical and complete (figs. 375, 376). About 280 tropical species in 7 genera.

7. *Polypodiaceae.* — Annulus vertical and incomplete (figs. 384, 385, 390). About 2000 species in 109 genera, including most of the ferns of ordinary observation in temperate regions.

It must not be supposed that the characters given above are the only ones used in separating the families. There are much more funda-

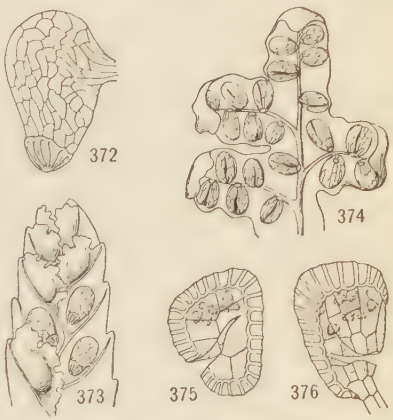


FIGS. 366–371. — Types of annulus: 366, sporangium of *Osmunda*, with a group of thick-walled cells representing the annulus, and a vertical line of dehiscence (after LUERSSEN); 367, sori of *Gleichenia*, showing relation to vein system and absence of indusium (after DIELS); 368, sporangium of *Gleichenia*, with equatorial annulus (after DIELS); 369, marginal sorus of *Hymenophyllum*, showing the stalklike receptacle bearing sporangia with an equatorial annulus, and the investing indusium (after KARSTEN); 370, 371, sporangia of *Trichomanes*, with equatorial annulus (after SADEBECK).

mental ones that will appear as the groups are considered. The sequence of the families as given represents the general relationship, the Marattiaceae being recognized as the most primitive in structure, while the Polypodiaceae are the most specialized and the most recent.

Sporophyte. — The sporophyte is characterized by a subterranean stem, except in the tree ferns, climbers, and epiphytes. In Marattiaceae this stem is short, tuberous, and radial, and covered by the persistent leaf bases (fig. 377). In the other families it is dorsiventral and more or less elongated (fig. 382), a habit apparently acquired by modern ferns, and derived from the older radial type.

Vascular system. — At least four kinds of vascular cylinder are represented in the stems of this great group, and there is much discussion as to their historical sequence. They are as follows: (1) the *protostele* (see p. 125), recognized as being the most primitive type (as in *Gleichenia*, fig. 378); (2) the *amphiphloic siphonostele*, in which the phloem occurs on both sides of the xylem in the pith-containing cylinder (as in *Adiantum*, fig. 379); (3) the *polystele*, in which several concentric bundles traverse the stele without organization into a definite cylinder (as in *Pteris*, fig. 380); and (4) the *ectophloic siphonostele*, in which the phloem occurs only on the outer side of the xylem in the pith-containing cylinder (as in *Osmunda*, fig. 381), which is thus composed of collateral bundles (p. 146). This last type of cylinder is regarded as the most advanced, since it is the characteristic cylinder of the majority of seed plants.



FIGS. 372–376. — Types of annulus: 372, sporangium of *Lygodium* with apical annulus (after PRANTL); 373, sporangia of *Lygodium* in position; some indusia shown (after SADEBECK); 374, sporangia of *Aneimia*, showing apical annulus and the vertical dehiscence (after SADEBECK); 375, 376, two views of sporangium of *Hemitelia*, showing the complete vertical annulus and the transverse dehiscence (after KARSTEN).

An important variation in the character of the xylem must be noted. The first xylem elements to appear are spiral vessels of small caliber. This initial group of vessels is called the *protoxylem*, and its position with reference to the subsequent xylem (*metaxylem*) is important to note. In a stele usually several protoxylem regions appear, and if all the metaxylem develops centripetally (towards the center of the stele), the xylem is *exarch*, which means that the protoxylem regions are external to the metaxylem. Exarch bundles are regarded as the most primitive, and are characteristic of all roots, of the protostele of *Lycopodium*, etc. If the metaxylem develops in all directions from the protoxylem, the xylem is *mesarch* (figs. 380, 381), which means that the protoxylem is surrounded by metaxylem. Mesarch bundles are very characteristic of ferns, and all of the four kinds of bundles described above as occurring among ferns are prevailingly mesarch. If all the metaxylem develops

centrifugally (away from the center of the stele), the xylem is *endarch*, which means that the protoxylem is internal with reference to the metaxylem. Endarch bundles are characteristic of seed plants, and are attained by some pteridophytes, as in Equisetales and Ophioglossales. A fern whose vascular cylinder is composed of collateral bundles resembles seed plants in this feature; but in such a case the bundle of

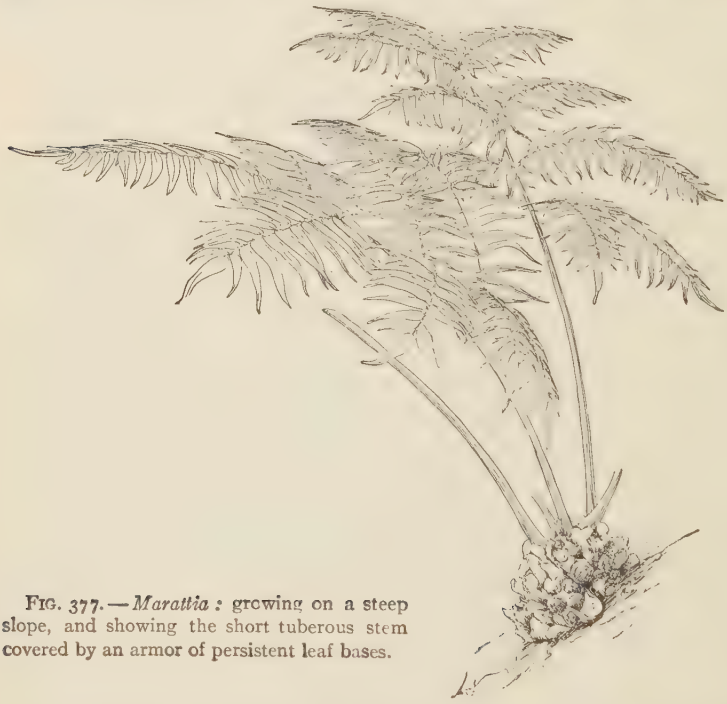


FIG. 377. — *Marattia*: growing on a steep slope, and showing the short tuberous stem covered by an armor of persistent leaf bases.

the fern is mesarch collateral, while that of the seed plant is endarch collateral. It must be remembered that to all such general statements in reference to great groups there are exceptions, and that the statement refers only to the prevailing condition in a group. Metaxylem must not be confused with the *secondary xylem*, which is formed by the cambium.

Another feature of the vascular cylinder of ferns is noteworthy. Where the leaf traces leave the cylinder to pass through the cortex, a gap immediately above the trace is left in the cylinder, which closes again further up. These *leaf gaps* are characteristic of the vascular cylinder of

Filicales and Ophioglossales, and they seem to be associated with the production of large leaves. On the basis of this character, these groups are said to be *phyllosiphonic*, as contrasted with the other groups of pteridophytes, which are *cladosiphonic*, meaning that they have branch

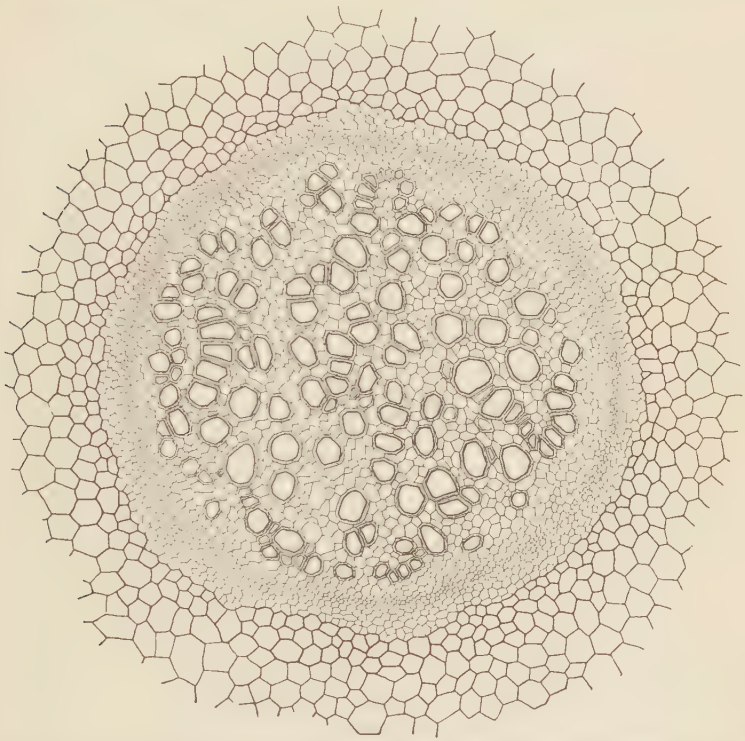


FIG. 378. — The protostele of *Gleichenia*: the xylem vessels, recognized by their large caliber and thick walls, occupy the entire central region of the stele; investing them is a zone of sieve vessels (phloem), which in turn are surrounded by the cortex.

gaps, but no leaf gaps. This distinction has been found to be a very important one in connection with the study of the origin of seed plants.

Leaves. — The leaves of ferns are the only aerial structures in ordinary terrestrial forms. They were formerly called *fronds*, with the idea that they were not ordinary leaves, but a combination of leaf and stem. They are usually branched, either pinnately or palmately, and are characterized by *dichotomous* (forking) venation (figs. 383, 386) and *circinate*

vernation (fig. 382), which means that the young leaf is enrolled from the tip downwards, and in expanding unrolls from the base upwards. The internal structure of the leaf is practically the same as that of the leaves of seed plants, with epidermis containing stomata, mesophyll (both palisade and spongy), and abundant veins (see p. 250).

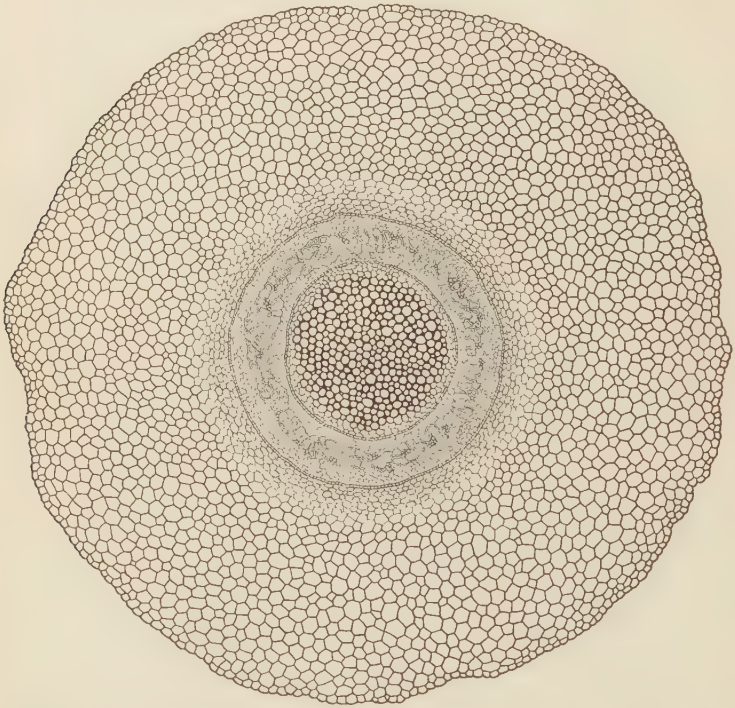


FIG. 379. — The amphiphloic siphonostele of *Adiantum:* beginning at the outside the general regions of the section are epidermis, a thick cortex, endodermis (the epidermis-like innermost layer of the cortex which bounds the stele), the outer phloem, the xylem, the inner phloem, the inner endodermis, and the pith.

Sporangia. — It will be impossible to describe all the methods of sporangium development, but the sporangia of Marattiaceae and Polypodiaceae will be described, with the understanding that the intermediate families show intergrading conditions.

Marattiaceae. — The Marattiaceae are eusporangiate, as are all the pteridophytes previously considered, and also the seed plants. Following the periclinal division of the superficial initial cell, the outer cell

develops a wall of several layers of cells, the innermost layer or two functioning as the tapetum; while the inner cell develops a large mass of sporogenous tissue. The number of mother cells in the different genera of Marattiaceae ranges from 128 to 2048, which means a theoretical output of 2048–8192 spores. Most of the Marattiaceae are further distinguished by the fact that the sporangia form what is called a

FIG. 380. — The polystele of *Pteris:* in the ill-defined stele there occur several (in this case thirteen) vascular bundles of varying size and form, each one of which is concentric (xylem surrounded by phloem) and invested by a distinct endodermis; in some of them the mesarch character is evident, the group of protoxylem elements (of small caliber) being more or less centrally placed (at least surrounded by metaxylem); the heavy-walled tissue represented by the three irregular masses associated with the vascular bundles is mechanical tissue.

synangium (fig. 386). These synangia appear like small groups of coalescent sporangia distributed over the surface of the leaf, as are the sori (see p. 165) in other ferns. In fact, in some of the Marattiaceae the sporangia are not in synangia, but form sori of distinct sporangia. It is evident that synangia and sori are equivalents; and it is probable that synangia are not coalescent sporangia, but rather sporangia that have not become completely separated from one another.

Polypodiaceae. — The Polypodiaceae are *leptosporangiate*, a peculiar feature belonging to all the Filicales except the Marattiaceae. It means that the sporogenous tissue is developed from the *outer* cell that follows the periclinal division of the superficial initial, instead of from the *inner*

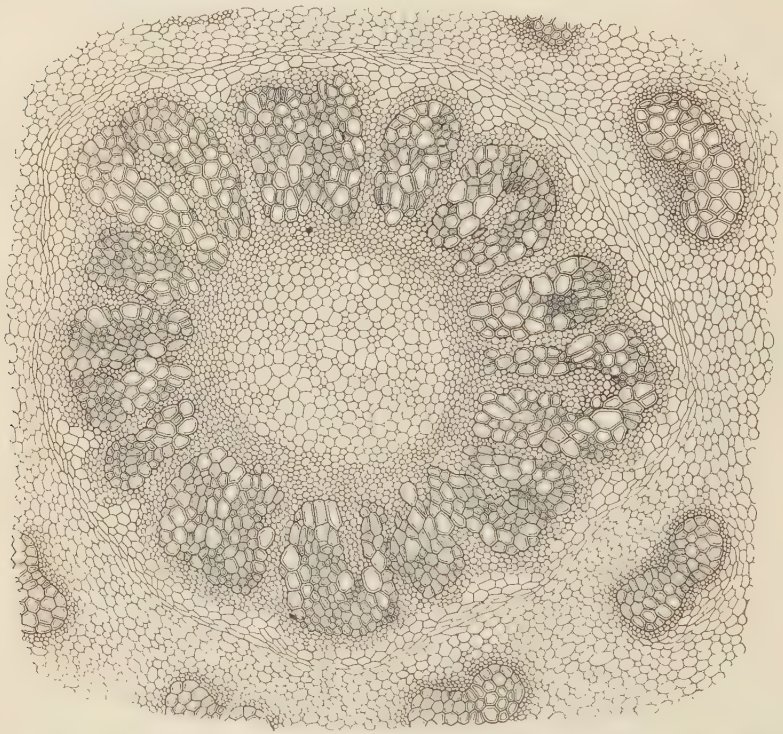


FIG. 381. — The ectophloic siphonostele of *Osmunda:* the central pith is surrounded directly by the xylem (internal phloem having disappeared), which occurs in distinct strands (separated from one another by the pith rays), the mesarch character of which is often very evident; investing the xylem is a thin sheath of phloem; the bundles shown in the cortex are sections of leaf traces.

cell, as in eusporangiates. The outer cell develops as a papillate-projecting cell (fig. 387), in which three oblique walls appear so as to form an apical cell with three cutting faces. This apical cell cuts off segments to form the elongated stalk. When segment formation ceases, a transverse wall through the apical cell cuts off a cap cell, and leaves a four-sided inner cell completely invested by the three uppermost segments and the cap cell. This centrally placed cell is the primary spo-

FIGS. 382–385. — *Aspidium:* 382, general habit, showing leaves and circinate vernation, dorsiventral (subterranean) stem, and secondary roots; 383, a single pinnule, showing dichotomous veins and sori with shieldlike indusia; 384, section through a sorus, showing the indusium and long-stalked sporangia; 385, a single sporangium, showing the incomplete vertical annulus and the transverse dehiscence. — After WOSSIDLO.

rogenous cell (fig. 388). The three uppermost segments and the cap develop the wall of the capsule, which is only one layer of cells thick. At the junction of the cap cell with the last segment is developed the *stomium*, which is a group of cells so arranged as to permit a cleavage in the wall of the capsule when it begins to dehisce. The *annulus* is a

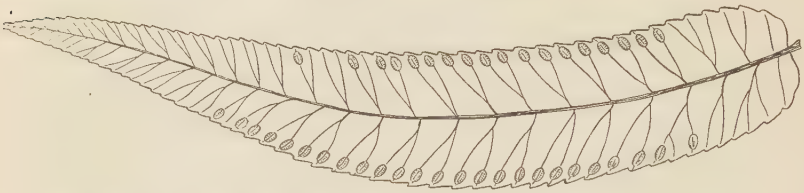
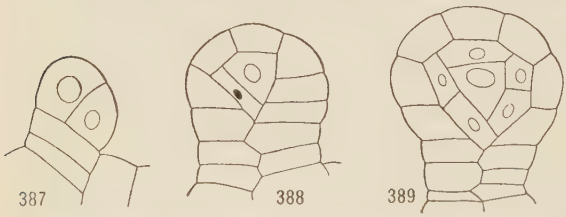


FIG. 386. — Leaflet of *Marattia*, showing dichotomous venation and synangia (instead of sori).

band of thick-walled cells which extends from the stomium over the top of the capsule and down on the other side to the stalk (figs. 385, 390).

The primary sporogenous cell cuts off a sterile cell from each one of the four faces, these four cells developing the tapetum (figs. 388, 389). The centrally placed sporogenous cell then begins a series of divisions until 16 mother cells are formed, which means a maximum output of 64 spores. Sometimes there are only 8, or 4, or even 2 mother cells. The tapetal cells break down, leaving the mother cells free in the enlarged cavity (fig. 390).



FIGS. 387–389. — Sporangium of one of the *Polypodiaceae:* 387, early stage, in which the outer papillate cell has begun to form the apical cell; 388, later stage, in which the cap cell and upper segments invest a central cell (primary spermatogenous), which has cut off one tapetal cell; 389, later stage, in which all the tapetal cells have been cut off and have begun to divide; the central cell, by a series of divisions, forms 16 mother cells.

These two kinds of sporangia, one from each extremity of the fern series, indicate not only a passage from the eusporangiate to the leptosporangiate habit, but also a striking reduction in the output of spores per sporangium. In this latter feature there is complete intergrading through the intermediate families.

In passing from Marattiaceae to Polypodiaceae, it is interesting to note the changes in the character of the sporangium stalk. Beginning with sessile sporangia, there is a transition to very short stalks, and finally the very long slender ones that characterize the Polypodiaceae are reached. This change in the character of the stalk accompanies the reduction in the output of spores, so that perhaps among leptosporangiate ferns the development of an elongated sporangium stalk is of more importance than a large output of spores from a single sporangium.

Fig. 390. — Mature sporangium of one of the *Polypodiaceae*, showing the incomplete vertical annulus and the transverse dehiscence.

Sorus. — The *sorus* is a feature of most Filicales, being a definitely limited group of sporangia (figs. 383, 384). Sori vary in form and in arrangement, and are useful as taxonomic characters. Sporangia do not always form sori; in some cases they are scattered over the surface of the leaf, in other cases they form in a continuous band along the margin.

Indusium. — The *indusium* is a flaplike outgrowth from the surface of the leaf which protects the developing sorus (figs. 369, 373, 383). It is exceedingly variable in form; in some cases forming a pouch, in others an overarching shield (fig. 383), in others a cup, etc. It is sometimes lacking entirely, and in certain cases it is replaced by the inrolled leaf margin, which is then spoken of as a "false indusium." These variations in the indusium are so constant for different groups as to be very useful as taxonomic characters.

Gametophyte. — The gametophyte of the Filicineae, better known as the *prothallium*, is a small green thallus, with rhizoids, and resembles the gametophyte of very simple liverworts (fig. 391). The most primitive ferns (Marattiaceae) have the largest and most massive gametophytes. In general, the development of the gametophyte passes through the stages indicated for liverworts (p. 98). In germination there protrudes from the spore a papillate outgrowth which is cut off by a wall as a cell and develops into the filamentous stage, the length of the filament being related to available light. Following this stage is that of the apical cell with two cutting faces, by means of which the gametophyte is broadened. Then follows the group of initials, by means of which the gametophyte is matured, in the course of which the usual apical notch is developed. The axial region of the gametophyte is much thicker than

the wings, giving a midrib appearance. In general the gametophytes are monoecious.

Antheridium. —The antheridia appear very early in the history of the gametophyte (fig. 392), being abundant even in the filamentous stage. In the mature gametophyte they occur on the ventral surface in the older part, among the rhizoids (fig. 391). No single type of development can

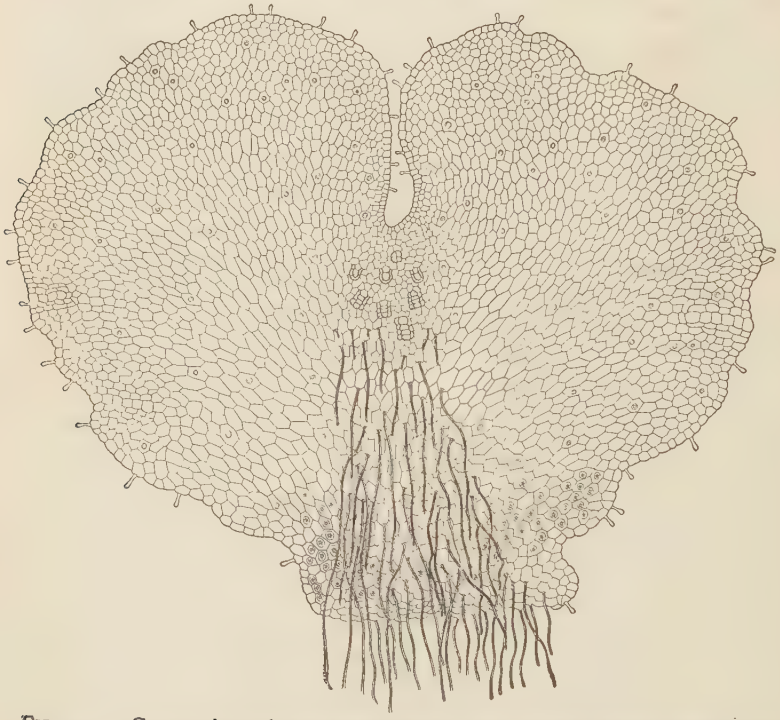


FIG. 391. — Gametophyte of *Aspidium*, looking at the ventral surface, which bears the sex organs and rhizoids; just behind the notch is a group of archegonia, and at the base of the thallus there are numerous antheridia.

be given for all the antheridia of Filicineae, for they are as variable in this regard as are the sporangia. The two extremes (Marattiaceae and Polypodiaceae) will be given, with the understanding that the intermediate families show intergrades.

Marattiaceae. — In the Marattiaceae there is the type of antheridium development usual among eusporangiates. The outer cell following the periclinal division of the superficial initial produces a wall consisting of

a single layer of cells; while the inner cell develops 100–200 or more sperm mother cells.

Polypodiaceae. — In the Polypodiaceae the antheridium is derived from the outer cell following the periclinal division, as in the case of the leptosporangiate sporangium. In this cell there appears first the *funnel wall*, which cuts off the *basal ring cell;* then the *dome wall* appears, intersecting the funnel wall and outlining the *central cell;* and finally the *cap* or *cover* cell is cut out of the dome cell, completing the *ring cell* (fig. 392). These divisions result in three peripheral cells investing a central one, the former producing the wall of the antheridium, the latter the sperm mother cells, usually thirty-two in number (sometimes sixty-four). There is thus a decrease in the output of sperms in passing from Marattiaceae to Polypodiaceae, just as in the case of the spores, but it is much less extensive. The sperm is large and spirally coiled, consisting of a large body (chiefly nucleus) and a conspicuous cytoplasmic beak, from which forty to fifty long retrorse cilia arise.

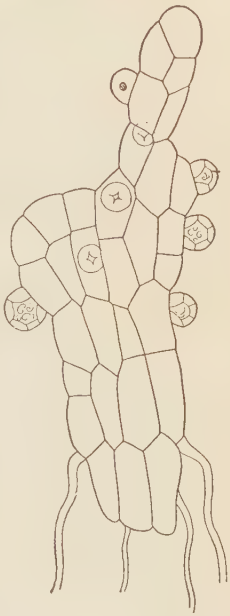


FIG. 392. — Young gametophyte of fern bearing antheridia; in the uppermost antheridium on the right side the funnel and dome walls have appeared; in the three other complete antheridia the cover cell has appeared, completing the three peripheral cells; the central cell has developed sperm mother cells.

Archegonium. — The archegonia appear late in the history of the gametophyte, being developed on the ventral side in the region of the apical notch (fig. 391). Their development is very uniform, and follows the usual course among pteridophytes. By a periclinal wall the superficial initial is divided into the primary neck cell and the inner cell; and by another transverse division the latter becomes the central cell and the basal cell (fig. 393, *a*). This row of three cells — primary neck cell, central cell, and basal cell — is perhaps the most commonly observed stage in the development. The primary neck cell produces a neck of three or four tiers (fig. 393, *b–d*), with four cells in each tier. The central cell produces the axial row, the first division resulting in the primary neck canal cell and the primary ventral cell. Among the Marattiaceae the primary neck canal cell produces two neck canal cells;

but among the Polypodiaceae usually only the nucleus divides, resulting in a single binucleate neck canal cell. The primary ventral cell divides, as usual, into the ventral canal cell and the egg (fig. 393, *c*). In passing from Marattiaceae to Polypodiaceae, one passes from broad canal cells to small ones, and from two distinct neck canal cells to the elimination of the wall (binucleate condition). There is thus a gradual disappearance

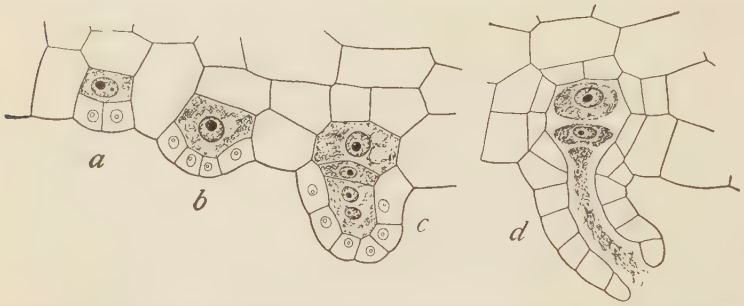


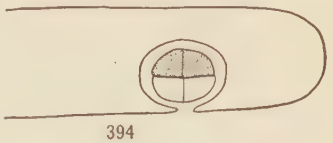
FIG. 393. — Archegonium of a fern: *a*, young stage, showing two neck cells, central cell (shaded), and basal cell, all from single initial; *b*, older stage, showing further development of neck and enlargement of central cell preparatory to forming the axial row; *c*, neck further developed and axial row complete (binucleate neck canal cell, ventral canal cell, and egg); *d*, mature archegonium, with neck complete, neck canal cell disorganized, ventral canal cell breaking down, and egg rounded off.

of the neck canal cells, a process which is completed when seed plants are reached.

Fertilization. — In fertilization the sperm enters the neck of the archegonium, ciliated end first; and then the ciliated beak ceases to function. As the sperm enters the cytoplasm of the egg, the cytoplasmic sheath of the sperm, including the beak, is often left behind, and the male nucleus moves alone through the egg cytoplasm to the female nucleus; but in some cases the whole sperm has been observed within the egg nucleus.

Embryo. — In the development of the embryo, the four great body regions are said to be differentiated at the quadrant stage; but in passing from Marattiaceae to Polypodiaceae the quadrants are directed differently. Among Marattiaceae the first division of the egg is transverse to the long axis of the archegonium (fig. 394), by far the most common plane. The current account is that this first division differentiates the shoot (stem and leaf) from the foot and root, the former being represented by the inner cell, the latter by the outer; and that at the quadrant stage the two outer (ventrally directed) quadrants develop the foot and

root, while the two inner (dorsally directed) quadrants develop the stem and leaf, which pierce through the tissue of the overlying thallus (fig. 394). Recent investigations, however, indicate that both the outer (ventral) quadrants may develop the foot, the two inner (dorsal) quadrants forming a tissue that gives rise to leaf, stem, and root. This method of development suggests that of the embryo of Ophioglossales, with which group the Marattiaceae seem to be closely allied.



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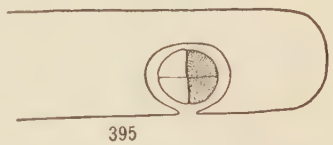

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FIGS. 394, 395. — Diagram of quadrant stage of embryo: 394, *Marattia*, in which the first wall is transverse to the long axis of the archegonium, the shaded quadrants giving rise to stem and leaf; 395, a polypod, in which the first wall is parallel with the long axis of the archegonium, the shaded quadrants (directed towards the notch) giving rise to stem (upper quadrant) and leaf (lower quadrant); in both cases the notch is to the right.

Among Polypodiaceae the first division of the egg is parallel with the long axis of the archegonium (fig. 395), the shoot cell being directed towards the apex (notch) of the prothallium. At the quadrant stage (fig. 395) the two apically directed quadrants give rise to stem and leaf (the latter being ventral); while the two basally directed quadrants give rise to foot and root (the latter being ventral). The stem and leaf, directed towards the notch, grow under the prothallium and the leaf turns up through the notch. In such a case, the foot is the most temporary organ, functioning only so long as the gametophyte endures, while the primary root does not exist for a long time. The relatively permanent structures of the sporophyte are the stem, giving rise to secondary roots, and the leaves.

Apogamy and apospory. — The phenomenon of *apogamy* is so prevalent among Filicineae that it deserves special mention. Apogamy is the production of a sporophyte by a gametophyte without the act of fertilization. Such a sporophyte may arise either from the unfertilized egg, in which case the apogamy is called *parthenogenesis;* or it may arise from the vegetative tissue of the prothallium, in which case it is called *vegetative apogamy*. It is found to be very common among ferns, and can be induced with little difficulty.

The companion phenomenon is *apospory*, in which a gametophyte is produced by a sporophyte without the formation of a spore. These

aposporous gametophytes in ferns arise usually from checked sporangia, but sometimes directly from the leaf margin (usually a tooth), and occasionally from other regions of the leaf.

An interesting question connected with apogamy and apospory is the effect on the number of chromosomes. A sporophyte has the double (diploid) number ($2x$) of chromosomes because it has come from a fertilized egg. Therefore, does an apogamous sporophyte have the reduced (haploid) number (x)? A gametophyte has the reduced number (x) because it has come from a spore produced by the reduction divisions. Therefore, does an aposporous gametophyte have the double number ($2x$)? Recent investigations, both among ferns and seed plants, indicate that both of these questions may be answered in the affirmative.

Conclusions. — The important features of this great group may be summarized as follows: There are represented all the pteridophyte types of vascular cylinder, from the most primitive to the most advanced; but the cylinders are peculiar among pteridophytes (Ophioglossales excepted) in being phyllosiphonic. The leaves are the most highly developed among pteridophytes (Ophioglossales excepted), being reduced in number and increased in size. The sporangia are multiplied on the lower surface of the leaves; there is very little differentiation of foliage leaves and sporophylls; and there is no organization of strobili. The conspicuous features are the development of the leptosporangiate habit, found in no other group of vascular plants (water ferns excepted); and along with this the appearance of a special kind of antheridium development. There is a gradual diminution of spore output per sporangium, and a corresponding diminution of sperm output; also a persistent retention of homospory. The gametophyte is a thallose, aerial structure. The line as a whole appears to be highly specialized, the only group containing the possibilities of the higher plants being the Marattiaceae, probably the oldest family.

(b) Hydropteridineae

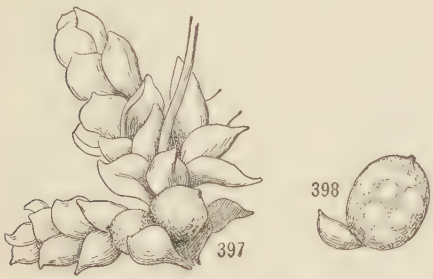
General character. — The water ferns are probably an aquatic branch from the true ferns that has developed heterospory. They are leptosporangiates, and hence are doubtless derived from the only other known group of leptosporangiates. They comprise two distinct families that seem to be of separate origin. It is evident, therefore, that heterospory has arisen independently in almost every group of pteridophytes.

Salviniaceae

These are the floating ferns, comprising two genera, *Salvinia* and *Azolla*, with few species, but some of them are widely distributed.

Sporophyte. — The sporophyte body is a floating, dorsiventral stem, that develops by an apical cell with two cutting faces, instead of the apical cell with three cutting faces usual among ferns. The segments are cut off right and left, and subsequent divisions result in eight rows of cells, four ventral and four dorsal. In *Salvinia* (fig. 396) the dorsal rows of cells give rise to four rows of broad, flat, overlapping, aerial leaves; while the two central ventral rows give rise to submerged and much dissected leaves that bear the sporangia. The two lateral ventral rows give rise to the branches, and roots are entirely lacking. In *Azolla* the two central dorsal rows of cells do not give rise to lateral members, but the two lateral dorsal rows produce leaves which are dorsiventrally lobed (fig. 397). The submerged ventral lobes bear the sporangia, and a chamber in the aerial dorsal lobe is inhabited by an endophytic alga (*Anabaena*). The two central ventral rows produce roots, and the two lateral ventral rows produce branches.

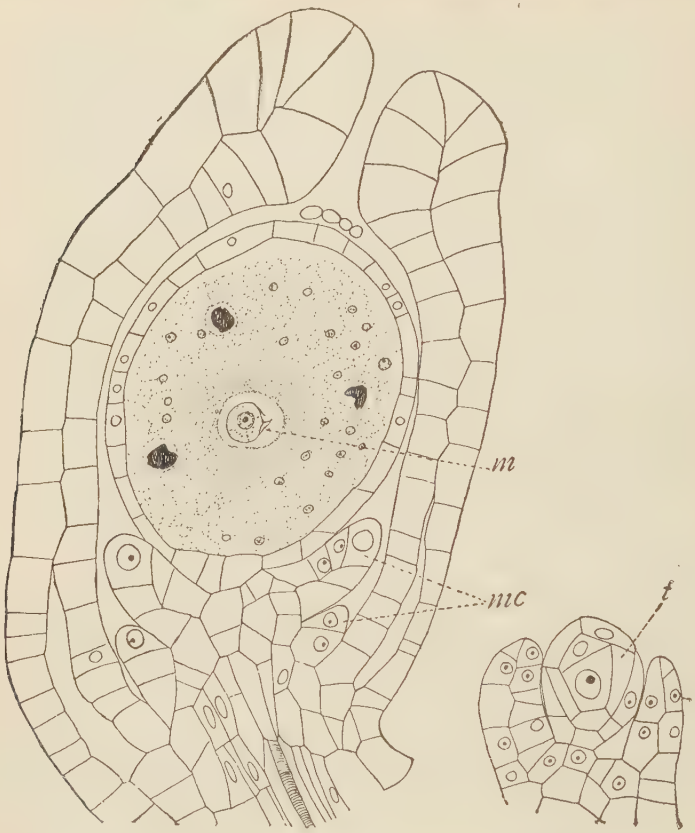
FIG. 396. — *Salvinia*, showing the broad floating leaves, and the dissected submerged leaves bearing sporocarps.



FIGS. 397, 398. — *Azolla*: 397, ventral surface of branch, showing leaves and sporocarps; 398, megasporocarp and microsporocarp. — After CAMPBELL.

Sporocarp. — The sporangia are submerged, as described, and each sorus is completely invested by the indusium,

which becomes hard at maturity, forming a small nutlike body called the *sporocarp* (fig. 396). In Salviniaceae, therefore, the sporocarp is a sorus invested by an indusium. Microsporangia and megasporangia



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FIGS. 399, 400. — *Azolla:* 399, young sporocarp, showing a young megasporangium and the developing indusium; the megasporangium has advanced to the cutting off of tapetal cells (*t*); 400, megasporocarp, showing the terminal megasporangium with one megaspore (*m*) surviving the degeneration of he others, and the microsporangia (*mc*) checked. — After MISS PFEIFFER.

begin to develop in each sorus, but only one kind matures, so that at maturity there are two kinds of sporocarps (*megasporocarps* and *microsporocarps*, fig. 398), both kinds occurring on the same plant and even on the same leaf segment. All the sporangia have long

slender stalks, and are distinctly leptosporangiate of the more advanced type.

In both kinds of sporangia sixteen mother cells are developed (eight in the megasporangium of *Azolla*), as among the most advanced of the true ferns. In the microsporangium sixty-four spores are formed; but in the megasporangium only one megaspore matures, a single mother cell functioning and three spores of the tetrad not maturing. Each sorus begins by developing a terminal megasporangium (fig. 399), and beneath this microsporangia begin to appear. The megasporangium of *Azolla* develops mother cells and forms eight tetrads (32 spores). If thirty-one of these megaspores degenerate and one persists, the microsporangia develop no further, and the structure becomes a megasporocarp containing one megaspore (fig. 400). If all thirty-two megaspores degenerate, the microsporangia continue to develop (fig. 401), and the structure becomes a microsporocarp (fig. 402).

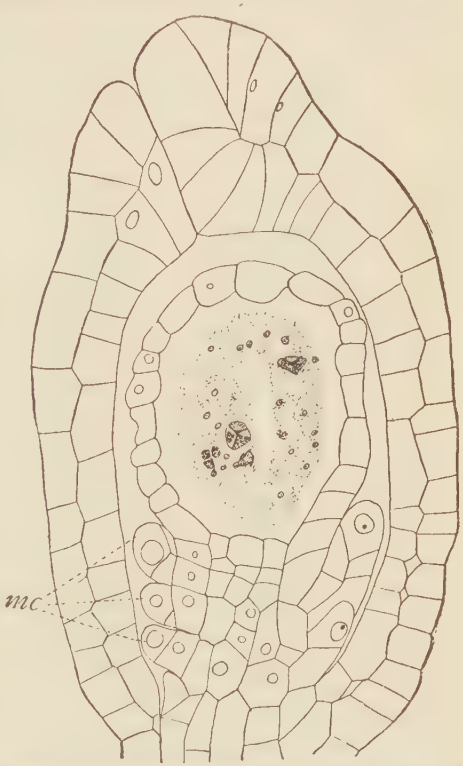


FIG. 401. — *Azolla:* young microsporocarp, in which all the megaspores have degenerated in the single megasporangium and the microsporangia (*mc*) are appearing in abundance. — After MISS PFEIFFER.

The tapetal cells break down and discharge their cytoplasm into the sporangial cavity, forming a remarkable matrix about the spores. In *Salvinia* the microspores lie firmly embedded in hardened cytoplasm; while in *Azolla* the cytoplasm organizes into two to eight masses (*massulae*), embedding the microspores. These massulae are invested by a

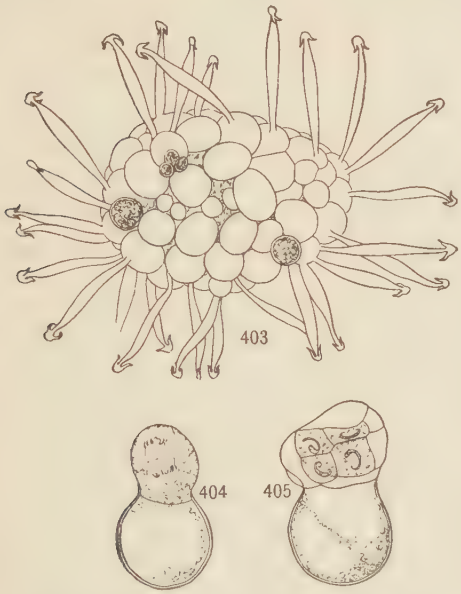
membrane, from the surface of which there arise remarkable appendages (*glochidia*) that resemble hairs with sagittate tips (fig. 403). About the single megaspore the matrix forms a heavy and often elaborate *perinium* (p. 147) or *epispore* (fig. 406).

Male gametophyte. — The microspore germinates within the sporangium of *Salvinia*, and within the discharged massulae of *Azolla*, in both cases sending out a tube to the surface, the external part of which is cut off by a wall (fig. 404). This external, water-exposed cell is the antheridium initial; and therefore the male gametophyte, as in *Selaginella* and *Isoetes*, is reduced to one vegetative cell (within the microspore) and one antheridium. The antheridium initial begins a series of two or three transverse divisions, after which a central cell is cut off by periclinal walls and produces eight sperm mother cells (fig. 405).

FIG. 402. — *Azolla:* older microsporocarp, in which the microsporangia have developed to the mother cell stage (*mcm*) and the terminal megasporangium has collapsed. — After MISS PFEIFFER.

Female gametophyte. — The development of the female gametophyte differs in several important particulars from that of *Selaginella* and *Isoetes*. The nucleus of the megaspore divides near its apex and a relatively small apical cell is cut off. The wall thus formed separates

the nutritive region from the reproductive region. The small apical cell protrudes through the megaspore wall and develops an exposed tissue containing archegonia (fig. 406). The nucleus of the large nutritive cell (almost the entire body of the megaspore) remains undivided in *Salvinia*, but in *Azolla* it initiates a series of free nuclear divisions, no cell walls



FIGS. 403–405. — *Azolla:* 403, massula, with inclosed microspores (shaded) and glochidia; 404, development of male gametophyte, the extruded cell (antheridium initial) beginning to divide; 405, male gametophyte with antheridium complete (wall cells enclosing spermatogenous cells). — After CAMPBELL.

FIG. 406. — *Azolla:* female gametophyte, showing the extruded, archegonium-producing tissue and the large nutritive cell (invested by the megaspore wall); around the gametophyte are remains of the perinium, and above a part of the indusium is represented. — After CAMPBELL.

being formed. The two chief points of contrast in this developmental history, as compared with *Selaginella* and *Isoetes*, are (1) the development of a wall across the spore in connection with the first nuclear division, forming a *diaphragm* between the nutritive and reproductive regions; and (2) the failure to develop a nutritive tissue.

Embryo. — The development of the embryo differs in no way from that of true ferns, except that the first division of the egg is transverse to the long axis of the archegonium, a feature characterizing the primitive Marattiaceae, but not the modern leptosporangiates.

FIG. 407. — *Marsilea*: showing dorsiventral stem giving rise to roots below and leaves above, circinate vernation of developing leaves, and adaxially borne sporocarps.

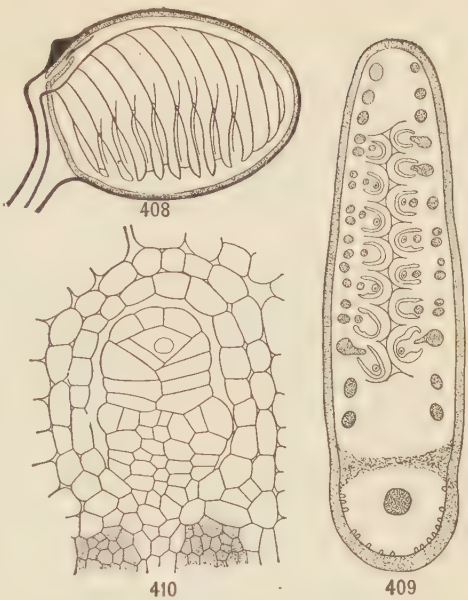
Marsileaceae

This family comprises the genera *Marsilea* and *Pilularia*, whose species root in the mud, under water or in muddy flats.

Sporophyte. — The stem is dorsiventral, as in the Salviniaceae, but it develops from an apical cell with three cutting faces, thus forming three longitudinal rows of segments. The leaves alternate from the dorsal segments, and the roots are produced by the ventral segments. The leaf of *Marsilea* has a long petiole and four leaflets peltately arranged (fig. 407); the first leaves, however, produce no blades, only the petiole developing, and this is the permanent condition in *Pilularia*.

Sporocarp. — The so-called sporocarp is borne on a stalk that arises adaxially from the leaf (petiole), the whole structure apparently being a spore-bearing branch of the leaf (fig. 407). This adaxial structure may have arisen as did that of the Ophioglossales;

that is, by the fusion of lateral branches (p. 152). The sporocarp seems to be a modified leaf blade or blades enclosing a group of sori (fig. 408). In *Marsilea* the sporocarp is somewhat bean-shaped, each sorus being in a cavity that extends from the ventral side towards the dorsal (fig. 409). Lining each cavity is a delicate indusium completely investing the sorus, which contains both microsporangia and megasporangia (fig. 410). In the microsporangia all the mother cells function in producing microspores; while in each megasporangium only one megaspore matures, as in the Salviniaceae. The sori are attached to a tissue which swells remarkably upon exposure to water, dragging the sori out, from the ventral side of the sporocarp, attached to a mucilaginous ring formed of the swollen tissue (fig. 411). In *Pilularia* the sporocarp is globular, four soral cavities extending from the base towards the apex, the microsporangia being above and the megaspo-



FIGS. 408–410. — *Marsilea:* 408, inside of one of the "valves" of the sporocarp, showing the system of veins, the short branches supplying the sori; 409, section through a sporocarp, showing the two rows of sori beginning to develop (terminal cell in each is a young megasporangium); 410, section through a young sorus, showing a developing megasporangium (cutting off tapetal cells) above, and a microsporangium initial appearing on each side below; the investing indusium is evident. — After JOHNSON.

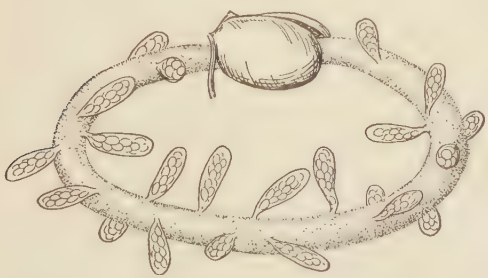


FIG. 411. — *Marsilea:* the swelling mucilaginous ring dragging out sori (indusia enveloping sporangia) from the sporocarp.

rangia below. There is also a swelling tissue which in this case bursts out at the top of the sporocarp. The remarkable longevity and resisting power of the sporocarps of *Marsilea* deserve mention. Sporocarps preserved on herbarium sheets for fifty years and others kept in 95 per cent alcohol have resumed activity when placed in water.

In contrasting the structures called sporocarps in Salviniaceae and Marsileaceae, it is evident that they are very different. In Salviniaceae

FIGS. 412–414. — Male gametophyte of *Marsilea:* 412, first division of the microspore into vegetative cell (the smaller) and antheridium initial; 413, first division of antheridium initial; 414, antheridium with wall of sterile cells investing spermatogenous cells (shaded). — After CAMPBELL.

the sporocarp is an indusium investing a sorus, while in Marsileaceae it is a leaf blade inclosing a group of sori with their indusia.

Gametophytes. — The male gametophyte does not emerge from the microspore, as it does in Salviniaceae, remaining entirely within the spore coat, as in *Selaginella* and *Isoetes*. As in all the previously mentioned cases of heterospory, a single vegetative cell and a single antheridium make up the male gametophyte (figs. 412–414); but in Marsileaceae the output of sperms is 32, much larger than in Salviniaceae (8) and in *Isoetes* (4). The sperms of *Marsilea* are remarkable for the great number of coils in the beak, reaching 13 or 14, the upper 12 or 13 having no cilia (fig. 415). The female gametophyte closely resembles that of the Salviniaceae, and the nucleus of the great nutritive cell remains undivided, as in *Salvinia* (figs. 416, 417).

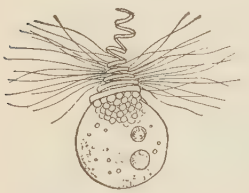
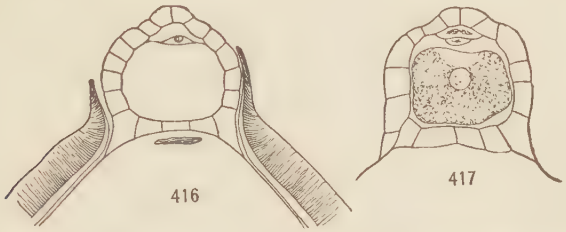


FIG. 415. — Sperm of *Marsilea*. — After CAMPBELL.

Embryo. — The embryo develops as in all the leptosporangiate ferns, the first wall of the egg being vertical (parallel with the long axis of the archegonium), and the four body regions being differentiated at the quadrant stage. It is noteworthy that the Marsileaceae have retained the primary vertical wall of the egg, characteristic of the leptosporangiate

ferns, and that Salviniaceae have the transverse wall of the older eusporangiate Marattiaceae.

Conclusions. — It is evident that the water ferns are a very specialized aquatic group, probably derived from the leptosporangiate ferns. Moreover, the features of the sporangium, in development and output, indicate an origin from one of the higher leptosporangiate families. The



FIGS. 416, 417. — Female gametophyte of *Marsilea:* 416, the tissue protruding from the heavy megaspore wall developing a single large archegonium; the top of the large nutritive cell with its single nucleus seen; 417, the mature archegonium. — After CAMPBELL.

annulus characters, which might have determined the point, are lacking. It is interesting if heterospory has developed in these aquatic conditions; and it is noteworthy that the development of the female gametophyte is very different from that of *Selaginella* and *Isoetes*, which resemble gymnosperms in this regard. The fern connections of Marsileaceae are clearer than those of Salviniaceae, which in habit are further removed from the terrestrial leptosporangiates.

CHAPTER IV — SPERMATOPHYTES

Introductory. — The Spermatophytes (seed plants) include the most highly organized plants, and are distinguished from the lower groups by the production of seeds. Once they were called *Phanerogams*, a name contrasted with *Cryptogams*, which included all the lower groups. *Phanerogam* means "sexual reproduction evident," and *cryptogam* means "sexual reproduction concealed." This distinction was based upon the belief that stamens and pistils are sexual organs, and that no such organs are evident in the lower groups. In fact, the sexual organs are very evident in the groups included under cryptogams; while they are very obscure in the so-called phanerogams.

The seed plants were also generally called *flowering plants*, but the flower is not a structure that defines the group. There are two possible definitions of a flower. A very common one is that it is essentially a group of sporophylls (stamens and carpels); but this definition includes the strobilus, a structure well represented among pteridophytes. Another definition of a flower is that it is a structure in which a perianth (sepals and petals) is associated with the group of sporophylls; but this definition excludes many seed plants, and especially all the gymnosperms. The limit of the flower, therefore, is either more extensive than seed plants or less extensive; and since the structure does not fit the group, the name flowering plants has been abandoned. The seed is a structure that seems to agree exactly with the boundary of the group, and therefore the name seed plants (spermatophytes) seems to be the most appropriate.

The two groups of spermatophytes are *Gymnosperms* and *Angiosperms*, the names expressing the conspicuous difference; for in gymnosperms the seeds are exposed, and in angiosperms they are enclosed in a case. This difference is very far from expressing the full contrast between these two groups, but the characters will be developed as the groups are described. It is sufficient to state here that the gymnosperms are very ancient and form a comparatively small part of the present seed plant vegetation; while the angiosperms are comparatively modern and include the great bulk of the present seed plant vegetation.

A. GYMNOSPERMS

This group includes the primitive seed plants, and to understand their relation to pteridophytes it will be necessary to consider them in their historical sequence. Seven great groups are recognized: (1) *Cycadofilicales*, (2) *Bennettitales*, (3) *Cycadales*, (4) *Cordaitales*, (5) *Ginkgoales*, (6) *Coniferales*, and (7) *Gnetales*. The first, second, and fourth of these groups are extinct.

(1) Cycadofilicales

Discovery. — The discovery of the existence of this most primitive group of seed plants, known only in the Paleozoic and chiefly in the Carboniferous, is so recent that a brief outline will be of interest. The Coal-measure deposits are notable for the remains of fernlike plants, and such plants constitute about one half of the known vegetation of the time. Until recently all of these plants were thought to be ferns, the evidence from their leaf forms and venation appearing to be conclusive. Most of them show no sporangia, and such sporangia as do appear are mostly of the *Marattia* type. The first expressed doubt (1883) that these fernlike plants were all ferns arose from the persistent absence of sporangia. Later the anatomy of the stems of several forms was discovered to show characters combining those of ferns and of cycads, and for such forms the group name *Cycadofilices* was proposed (1899). In 1903 seeds were found on the leaves of certain of these Cycadofilices, and the group name *Pteridosperms* was proposed to include the Cycadofilices that bear seeds. Finally, in 1905 the microsporangia were discovered; and curiously enough some of these microsporangia were the sporangia of so-called ferns. Therefore, a knowledge of the existence of ferns during the Carboniferous came to depend more upon inference than upon any sure recognition of their remains. In any event, it seems certain that almost all of the so-called fern vegetation of the Carboniferous belongs to these primitive seed plants. The oldest name for the group is here adopted, its termination being adapted to that of the other groups with which it is coordinate.

Sporophyte. — The habit of the sporophyte body is conspicuously fernlike, including not merely the usual fern habit, but also climbers and trees. The vascular anatomy, which first separated the group from ferns, deserves brief mention. Three of the four conspicuous types of vascular cylinder found among ferns (see p. 156) are found in the stems of Cycadofilicales, the three representative genera illustrating them be-

ing *Heterangium* (protostele), *Lyginodendron* (ectophloic siphonostele), and *Medullosa* (polystele). Among the Cycadofilicales, however, there is a development of secondary wood in varying amount, but always distinct (fig. 418). This character distinguishes Cycadofilicales from ferns, but it would not serve to separate them from pteridophytes, for secondary wood was formed by many of the older pteridophytes (as the extinct Lycopodiales and Equisetales).

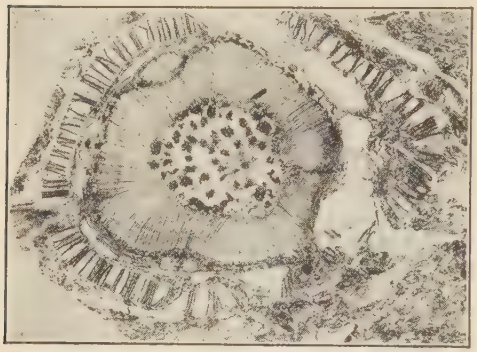


FIG. 418. — Photograph of cross section of vascular cylinder (ectophloic siphonostele) of *Lyginodendron*, showing the secondary wood characteristic of Cycadofilicales. — Photograph by BOODLE.

Seeds. — The seeds of Cycadofilicales have now been found in connection with all the great frond genera of the Carboniferous. The leaves or the pinnae which bear seeds usually differ in form from the sterile

419

420

FIGS. 419, 420. — Seeds of Cycadofilicales: 419, seed of *Lagenostoma Lomaxi* (restored by OLIVER), showing the investing glandular cupule; 420, two seeds of *L. Sinclairi* terminating naked branches. — After ARBER.

leaves or pinnae, the seeds terminating naked branches and often being invested by husklike cupules (figs. 419, 420, 421), as if the

lamina had disappeared and only the prominent ribs persisted. In some cases, however, the seeds replace sori on ordinary fernlike leaves (fig. 422). There are very many detached paleozoic seeds which have never been connected with the plants that produced them; but doubtless many of them belonged to the Cycadofilicales. So far as these attached and detached seeds have been sectioned, they show certain features in common which are regarded as primitive. In seed plants the megasporangium has long been called an *ovule*. In general structure it consists of a central region (the real sporangium) called the *nucellus*, which is invested by one or two coats called *integuments*. A passageway (*micropyle*) is left through the integument at the tip of the nucellus. When the changes occur that transform the ovule into the seed, the integument develops in various ways to form the seed coat or *testa*. In fossil seeds it is evident that the structure of the ovule must be inferred from the structure of the seed.

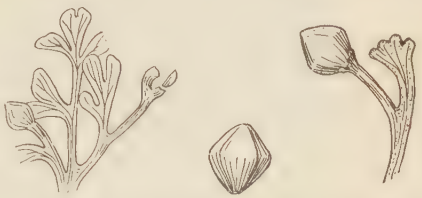


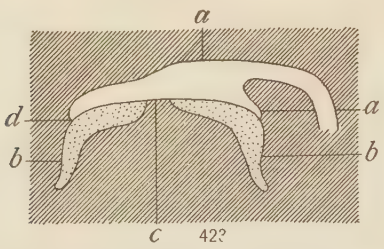
FIG. 421. — Seeds of *Ancimites* (an American form). — After WHITE.

FIG. 422. — Seeds of *Pecopteris* on ordinary fernlike leaves. — After GRAND' EURY.

In the seeds of Cycadofilicales there is a three-layered testa, which is often peculiarly free from the nucellus. The vascular strand that enters the seed divides into two sets of branches, one set traversing the testa, and the other traversing the outer region of the nucellus, in case the testa and nucellus are free. The nucellus is beaked, and contains a deep chamber (*pollen chamber*), which serves as a gathering place for microspores, and which in living gymnosperms is associated with swimming sperms. A remarkable feature of the seed, and of all paleozoic seeds that have been sectioned, is that there is no trace of an embryo. Since the embryo is present in mesozoic seeds, its absence from paleozoic seeds must be due to other causes than failure to be preserved.

Stamens. — The microsporangiate structures (stamens), first recognized in 1905, have been found to be of at least three types. They are

leaves or pinnae more or less modified, and may be said to take the following forms: (1) epaulet type (*Crossotheca*), in which the microspo-



FIGS. 423, 424. — Microsporangia of Cycadofilicales, epaulet (*Crossotheca*) type: 423, diagram of cross section, showing the limb (*a*), the sporangia (*b*) showing their attachment (*d*), and the "central boss" (*c*); 424, diagram of horizontal section, showing the two-chambered sporangia; letters as before. — After KIDSTON.

rangia are pendulous from a more or less peltate and stalked lamina (figs. 423, 424); (2) cupule type (*Calymmatotheca*), in which the microsporangia occur in cupule-like structures terminating naked branches (fig. 425); and (3) synangium type, in which the microsporangia occur as synangia upon the abaxial face of fernlike leaves.

FIG. 425. — Microsporangia of Cycadofilicales, cupule (*Calymmatotheca*) type: *Codonotheca;* sporangia on the inner surface of the cupule valves. — After SELLARDS.

Female gametophyte. — The female gametophyte is hardly at all preserved, so far as found, and sections of the seed give no evidence as to its structure.

Conclusions. — The chief features of this most interesting group may be summarized as follows: It is evidently very closely related to the ferns, the resemblance in external appearance being remarkably close. The vascular anatomy is distinctly of the fern type, but with the additional feature of secondary wood, which is a gymnosperm feature. The microsporangia are hardly changed from fern sporangia; but the megasporangia are enormously changed, a well-developed ovule replacing a sorus or a synangium. It seems clear that this, the most ancient group of seed plants, was derived from still more ancient ferns.

(2) Bennettitales

General character. — The members of this extinct group were very conspicuous during the Mesozoic, and they have been called fossil cycads. In fact, the Mesozoic has been called the age of cycads, so far as plants are concerned. Recent investigations have shown, however, that the Bennettitales are very distinct from the living cycads. They were extraordinarily abundant during the Jurassic, numerous remains having been found in North America, Europe, and Asia, and extending into the arctic regions. The richest display of forms occurs in the United States (Maryland, South Dakota, and Wyoming), the conspicuous American genera being *Cycadeoidea* and *Cycadella*, and in Mexico.

Sporophyte. — The sporophyte body is generally tuberous in form, sometimes very large, but short columnar trunks (three to four meters high) also occur. This stem is covered by a heavy armor of leaf bases, among which there are wedged numerous short axillary branches, each bearing a terminal strobilus (fig. 426). The occurrence of numerous strobili on lateral branches is in striking contrast with the usually solitary terminal strobilus of the cycads. A second striking external feature is the occurrence of an abundance of membranous scales (*ramentum*), which are packed among the leaf bases and sometimes sheath the whole body with a feltlike mass. This ramentum is characteristic of ferns, and is often conspicuous upon the trunks of tree ferns. The anatomy of the stem is exactly like that of the cycads; with a very thick cortex, a comparatively thin vascular cylinder, and a large pith. The vascular bundles composing the cylinder are collateral, with the protoxylem in contact with the pith (endarch). In the leaves, however, the protoxylem

Fig. 426. — Photograph of fossil trunk of *Cycadeoidea*, showing the tuberous body and the armor of leaf bases, wedged among which may be seen numerous strobili. — After Wieland.

occurs in the midst of the xylem (mesarch), a feature characteristic of ferns. The wood of the stem, therefore, has advanced to the endarch condition, while in the leaves the old mesarch character of the ferns remains. The leaf trace is a single and direct vascular strand, in striking contrast with the leaf traces of cycads. The tuberous or columnar body bears a crown of huge cycad-like (fernlike) leaves.

FIG. 427. — Diagram of strobilus of *Cycadeoidea*, showing the hairy sheathing bracts, the set of branched stamens (bent inward so that the backs are towards the ovules), and the tip of the axis covered by ovules. — After WIELAND.

Strobilus. — The strobili of certain European forms have been known for a long time, but their real structure was not known until the recent study of the American forms. It seems clear now that probably the strobili of the whole group were bisporangiate, a most remarkable condition among gymnosperms, for in all the other groups the strobili are either staminate or ovulate, except in cases that are regarded as abnormal. The structure of a representative strobilus may be described as an illustration of the general condition (figs. 427, 428). The strobilus is sheathed by a series of sterile, overlapping bracts. Within (and above) these there arise ten to twenty microsporophylls (stamens); and within the stamens, covering the rest of the axis of the

strobilus, are the megasporophylls (carpels). The whole structure is like that of a huge flower (like a *Magnolia*), with perianth, stamens, and conical mass of carpels. When the stamens are present, the ovules are immature; when the seeds are mature, the stamens have disappeared, but their place of insertion is evident in the form of a shoulder between the seeds and the enveloping bracts (fig. 429).

FIG. 428. — Diagram of strobilus of *Cycadeoidea*, showing the relation of parts and a stamen unfolded. — After WIELAND.

Stamens. — The stamens are like fern leaves that are twice pinnate (fig. 428), and underneath the pinnules (sometimes twenty in number) there are two lateral rows of synangia (fig. 430), which are sori of the *Marattia* type. The stamens are united below into a broad disk, becoming free and pinnate above the ovule-bearing apex of the axis. The synangia are almost identical in structure with those of *Marattia*, so

that the microsporangia have advanced very little beyond the fern level.

Ovulate structures. — The megasporangiate structures, however, have advanced very far beyond the fern level, and are very peculiar (fig. 431). The seeds terminate long and slender stalks, which are packed among *interseminal scales* that are also stalked structures. The stalked seeds and interseminal scales are arranged so as to form an ovoid, fruitlike body, with a mosaic surface composed of the flaring tops of the interseminal scales, wedged between which the micropylar tubes of the seeds protrude. If this structure be compared with the seed-bearing structures of the Cycadofilicales, especially those in which the seeds terminate the naked branches of a pinna, it will be observed that if these branches be reduced to a single axis, the condition in Bennettitales is obtained. The interseminal scales are probably sterile megasporophylls; and all the megasporophylls, leaflike and spreading in Cycadofilicales, are compacted into a strobilus in Bennettitales.

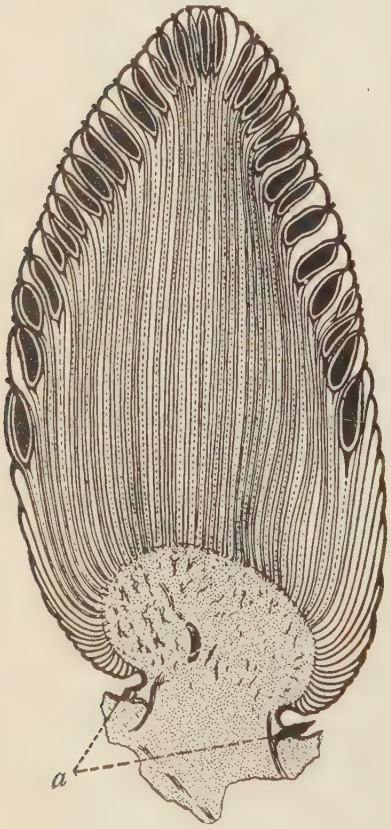


FIG. 429. — Strobilus of a species of *Cycadeoidea*, in which the seeds are mature, and showing the shoulder (*a*) which bore the stamens. — After WIELAND.

Seeds. — The structure of the seeds has been obtained from sections, which show a basal cupule, suggesting a rudiment of the investing and husklike cupule of some of the Cycadofilicales; a two or three layered testa; and a large dicotyledonous embryo completely filling the seed (fig. 432). This embryo is unlike that of any living gymnosperm, in that in developing it destroys all of the endosperm (see p. 202).

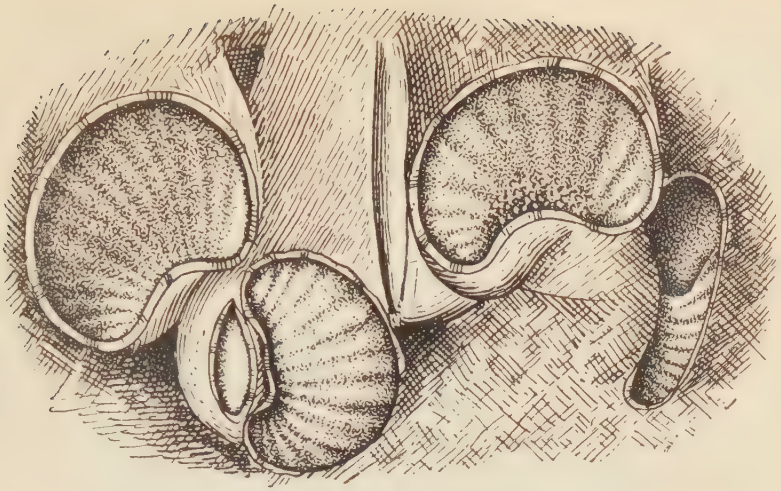


FIG. 430. — Microsporangia (synangia) of *Cycadeoidea*. — After WIELAND.

FIG. 431. — Diagram of strobilus of *Bennettites*, in which the seeds are mature; showing the sheathing bracts, the long-stalked seeds, and the broad-tipped interseminal scales. — After SOLMS and POTONIÉ.

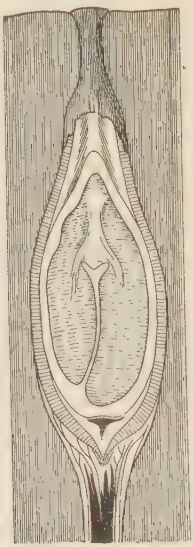


FIG. 432. — Section of a seed of *Bennettites*, showing the large dicotyledonous embryo. — After SOLMS.

Conclusions. — The characters presented by this group are a combination of the characters of Cycadofilicales, of Cycadales, and of characters peculiar to itself. In lateral branches, ramentum, direct leaf traces, and synangia, it resembles Cycadofilicales and Filicales. In general habit and anatomy it resembles Cycadales. In its bisporangiate strobilus, its united and pinnate and synangium-bearing stamens, its mixture of sterile and fertile megasporophylls bearing terminal ovules, and its peculiar embryo, it is unlike any other gymnosperm group.

FIG. 433. — *Cycas media* (middle and right) and *C. Normanbyana* (left), from oriental tropics. — After F. VON MÜLLER.

(3) CYCADALES

General character. — The cycads are tropical plants, including almost one hundred species, constituting nine genera. They are distributed almost equally between the oriental and occidental tropics, *Cycas* being the conspicuous oriental genus, and *Zamia* the conspicuous occidental one. The cycads are the modern living representatives of the line that began with the Cycadofilicales of the Paleozoic, and was continued by the Bennettitales of the Mesozoic.

Sporophyte. — The sporophyte body consists of a tuberous or columnar stem, covered by an armor of leaf bases, and bearing a crown of large branched leaves and an apparently terminal strobilus (figs. 433–437). All the stems are tuberous when young, but in some species the tuberous body passes into the columnar, which in certain species of *Cycas* reaches

FIG. 434. — *Dioon edule* (Mexican). — After CHAMBERLAIN.

a height of 10 or even 20 m. (fig. 433). In those forms with the persistently tuberous habit, the stem is sometimes subterranean and very small (fig. 437). While the stem usually appears to terminate in a single strobilus, the strobili are in fact lateral, although close to the apex, and a succession of them may appear near the stem tip. In fact, in an African form strobili have been observed arising in a cycle about the vegetative point. It will be remembered that the strobili of Ben-

nettitales are lateral, but distributed along the stem; while in Cycadales they are lateral, but restricted to the tip of the stem.

Vascular anatomy. — The anatomy of the stem resembles that of the Bennettitales, with a thick cortex, a thin vascular cylinder, and a large pith (fig. 438). The vascular bundles of the stem are collateral and endarch, as usual among gymnosperms; but in leaf traces, or leaf veins, or axes of strobili, the old fern connection is indicated by mesarch bundles and sometimes even by concentric bundles. It is in these so-called peripheral regions of the body that the older features of the vascular structure persist the longest. The primary cambium of the stem may persist (as in *Zamia*), although the amount of secondary wood it forms is always small; or it may be of short duration (as in *Cycas*), in which case a series of successive cambium cylinders is formed in the cortex, resulting in a concentric series of vascular cylinders. The leaf traces differ very much from those of the Bennettitales. Instead of being direct, as in the latter group, some of them (usually two) pass around the stem through the cortex, and often enter a leaf on the opposite side of

FIG. 435. — *Bowenia* (oriental), showing tuberous stem with heavy armor of leaf bases. — After EICHLER (ENGLER and PRANTL).

the stem from their emergence from the cylinder. These leaf traces curving about through the cortex are called *girdles*, and are conspicuous objects in any cross section of the stem (fig. 438).

Leaves. —The leaves are very large, pinnate, and generally leathery. The mesophyll is peculiar in containing cells elongated parallel with the leaf surface, and so loosely arranged as to appear like bridles of tissue traversing a large cavity.

Strobilus. — The strobili are dioecious, in striking contrast with those of Bennettitales, in which the staminate and ovulate structures are not only on the same plant, but also in the same strobilus.

FIG. 436. — *Zamia* (from Florida), showing small, tuberous, mostly subterranean stems, one bearing a staminate strobilus.

FIG. 437. — *Zamia*, bearing an ovulate strobilus.

Staminate. — In the staminate strobili the sporophylls are closely imbricate (figs. 436, 439), narrowed below, and broadened above into

a more or less expanded terminal sterile portion (figs. 440, 441). The sporangia are borne on the abaxial surface of the sporophyll, varying in number from 1000 or more in *Cycas* (fig. 440) to very few in *Zamia* (fig. 441). They may cover the whole face of the sporophyll, or may occur only on the two flanks. Usually they are in definite sori of two to six sporangia, and often they are more or less united at base.

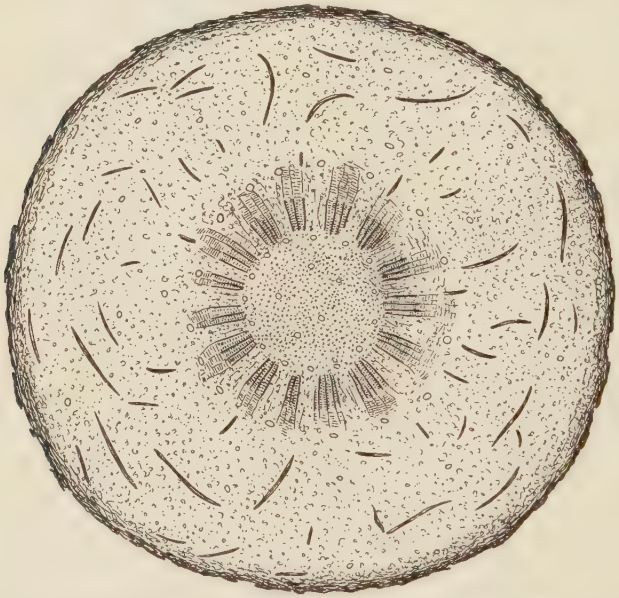


FIG. 438. — Cross section of a stem of *Zamia*, showing the thick cortex, thin vascular cylinder, large pith, and curving leaf traces (girdles); the vascular cylinder is seen to consist of vascular bundles (xylem next the pith, phloem next the cortex) separated by pith rays; partly diagrammatic.

The sporangia are eusporangiate in development, but the initial cell or cells are *hypodermal* (under the epidermis), and not superficial as among the pteridophytes. The initials usually form a hypodermal plate of four cells which divide periclinally into two plates, the outer giving rise to the four to seven wall layers (overlaid by the epidermis), the inner giving rise to the mass of sporogenous tissue. The tapetum is organized from the peripheral layer of sporogenous cells. The output of spores per sporangium varies from 500 in *Zamia* to 26,000 in *Encephalartos*.

The abaxial distribution of sporangia, the sori, the large output, the dehiscence, all resemble ferns of the *Marattia* type.

Ovulate. — The ovulate strobili (fig. 442) are sometimes very large. The genus *Cycas* is peculiar in its ovulate strobilus, in that it is not a compact strobilus, but a rosette of sporophylls resembling reduced foliage leaves, in which ovules replace the lower pinnae or teeth (figs. 443, 444). In general, the sporophylls vary from the leaflike (pinnate) forms of *Cycas* to peltate forms (as in *Zamia*, fig. 441, and *Ceratozamia*, fig. 445). Between these extreme forms there is a complete series of transitions, but there is always a terminal sterile region of varying form. The ovules vary in number from five or six to two.

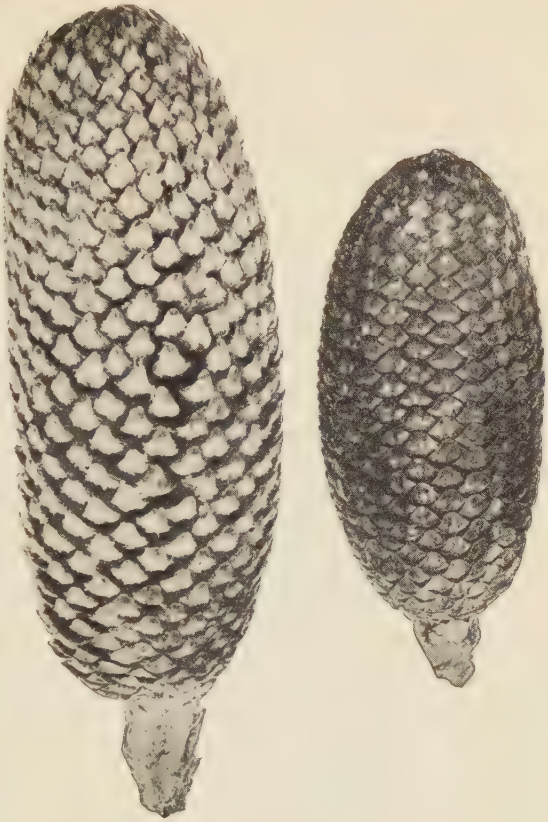


FIG. 439. — Staminate strobili of *Dioon*. — After CHAMBERLAIN.

FIGS. 440, 441. — Stamens (microsporophylls) of *Cycas circinalis* (440) and *Zamia integrifolia* (441). — After RICHARD.

Ovules. — The structure of the ovule (fig. 446) is of the same general type as those of Cycadofilicales and Bennettitales. The thick integument is free from the nucellus in the region of the nucellar beak, and develops a testa of three layers : a stony layer between an outer and an inner fleshy layer. Among the Cycadofilicales, it will be remembered, the vascular supply to the ovule is divided into two sets of vascular strands, the outer set traversing the integument, the inner set the peripheral region of the nucellus; but in that case the integument and nucellus are almost completely free. Among the Cycadales, where the integument and nucellus are free only above, the outer set of vascular strands traverses the outer fleshy layer of the testa and the inner set traverses the inner fleshy layer (fig. 446). The nucellus develops a sharp beak, within which a conspicuous pollen chamber is formed. The first evidence of sporogenous tissue is the appearance of a spore mother cell deep within the nucellus, which soon differs conspicuously from the neighboring cells in size and contents. This mother cell, by the reduction divisions, forms a linear tetrad, the innermost megaspore functioning, and in its growth encroaching upon the other megaspores and the neighboring cells.

FIG. 442. — Ovulate strobilus of *Zamia*.

Female gametophyte. — The female gametophyte develops in a general way as in *Selaginella* and *Isoetes*, and as in nearly all gymnosperms. At least five stages in the development should be borne in mind : (1) free nuclear division, by which a varying number of free nuclei are distributed through the cytoplasm of the megaspore; (2) parietal placing of these nuclei by the development of a central vacuole; (3) continued free nuclear division; (4) formation of parietal tissue by

the development of cell walls separating the free nuclei; (5) centripetal growth of this tissue until it fills the cavity of the enlarging megaspore (which is now known as the *embryo sac*, fig. 446). At least two regions

FIGS. 443, 444. — Megasporophylls of *Cycas:* 443, *C. revoluta;* 444, *C. circinalis.*

may be distinguished in the completed gametophyte; a region of smaller cells at the micropylar end of the embryo sac, in which archegonia are developed; and a deeper region of larger cells, which are nutritive in function (compare *Selaginella*, p. 136).

Archegonia. — The archegonia vary widely in number, but three to five are most common. The archegonium initial is a superficial cell, which divides periclinally into a primary neck cell (the outer one) and a central cell (the inner one).

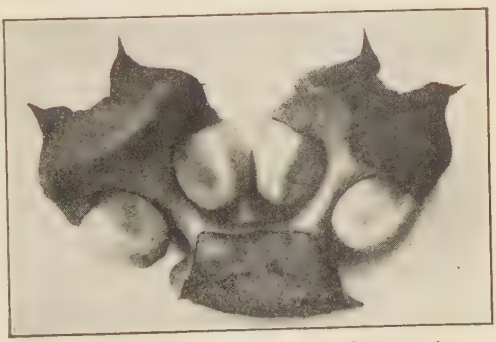


FIG. 445. — Megasporophylls of *Ceratozamia.*

The primary neck cell divides vertically, and these two neck cells, lying side by side, are constant among the Cycadales. The central cell then begins a remarkable enlargement, and becomes invested by a special jacket of cells, known as the *archegonial jacket*, which functions as a nutritive layer. Finally the nucleus of the central cell divides into the ventral nucleus, which soon disorganizes, and the egg nucleus, about which the cytoplasm is organized to form the egg (fig. 447). The notable feature of this archegonium, in contrast with the archegonia of bryophytes and pteridophytes, is the complete elimination of neck canal cells. The cycad egg and its nucleus are the largest known among plants. As the

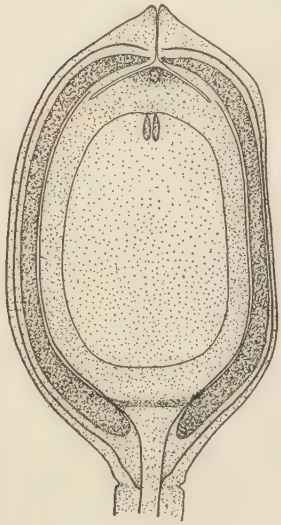


FIG. 446. — Diagrammatic section of ovule of *Dioon*, showing the thick integument free from nucellus at beak (in which the pollen chamber is evident, but not open); the three layers of the testa, outer fleshy (traversed by vascular strands), stony (thick and shaded), and inner fleshy (distinct in region of beak, but merged with nucellus below, and traversed by vascular strands); the embryo sac containing the female gametophyte (endosperm), in which two archegonia are present. — After CHAMBERLAIN.

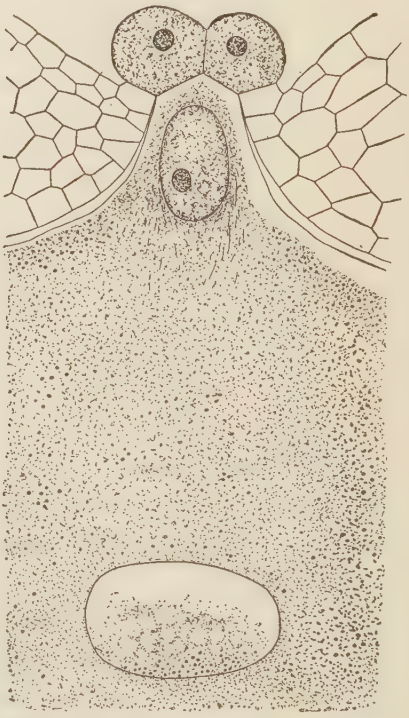


FIG. 447. — Micropylar end of a mature archegonium of *Dioon*, showing the two neck cells, the ventral nucleus (in the apex), and the egg nucleus (below). — After CHAMBERLAIN.

archegonium develops at the micropylar surface of the gametophyte, the neighboring cells continue growth, and the archegonium is left in a depression known as the *archegonial chamber* (fig. 448).

Male gametophyte. — The male gametophytes differ from those of *Selaginella* and *Isoetes* in certain important particulars. The first division within the microspore (pollen grain) cuts off a persistent vegetative cell. The next division gives rise to the *generative cell* (primary spermatogenous cell) and the *tube cell*. This is the usual condition of the gametophyte at the shedding of the pollen grain, which is therefore seen to contain three nuclei: those of the persistent vegetative cell, of the generative cell, and of the tube cell (fig. 449).

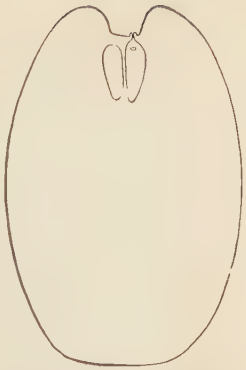
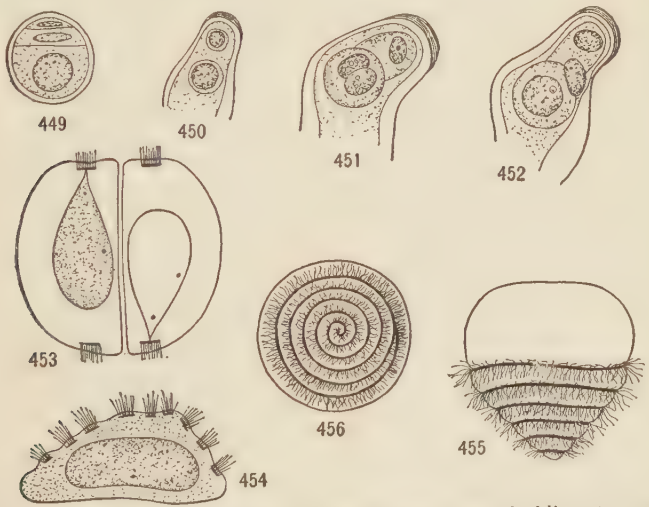
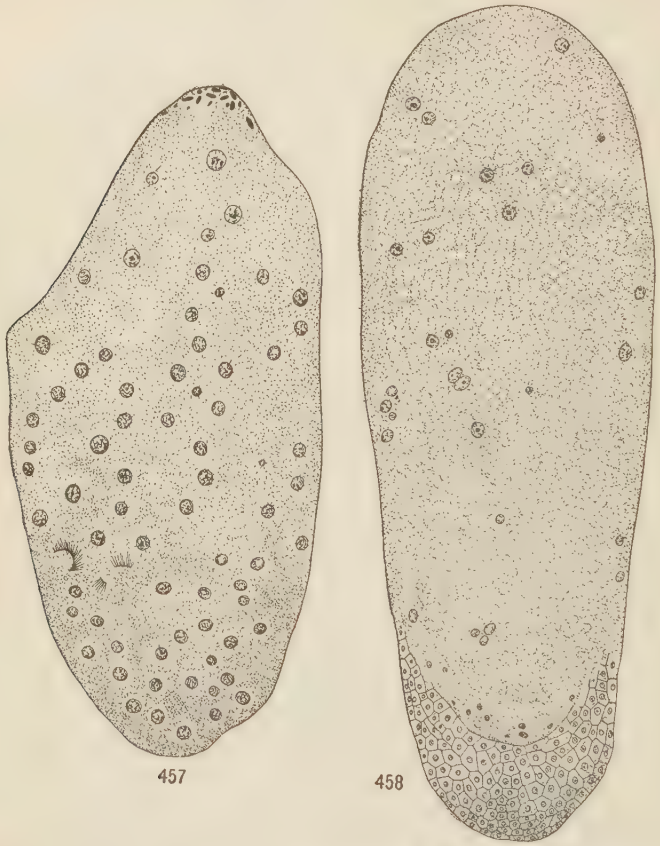


FIG. 448. — Diagram of embryo sac (containing female gametophyte) of *Dioon*, showing two archegonia and the archegonial chamber. — After CHAMBERLAIN.



FIGS. 449–456. — Male gametophyte of *Cycas revoluta:* 449, shedding stage of microspore (pollen grain), showing persistent vegetative cell, generative cell, and tube cell; 450, later stage (after shedding), showing rounded-off vegetative and generative cells (tube nucleus has passed into the pollen tube); 451, division of nucleus of generative cell into nuclei of stalk and body cells; 452, enlargement of nucleus of body cell, and thrusting out of the stalk nucleus; 453, division of body cell to form the two sperm mother cells, in each of which a ciliated sperm is beginning to form; 454, section of a developing sperm; 455, 456, two views of a mature sperm. — 449–454, after IKENO, 455, 456, after COULTER.

The subsequent development of the gametophyte occurs after the pollen grain has reached the pollen chamber. In this position the tube begins to develop and to penetrate the tissue of the nucellus, the tube nucleus passing into it. Then the generative cell, remaining within the



FIGS. 457, 458. — Development of the embryo of *Zamia:* 457, the stage of free nuclear division; 458, tissue-formation at base of egg, with numerous free nuclei remaining in the general cytoplasm. — After COULTER and CHAMBERLAIN.

grain, divides into the *stalk cell* and the *body cell* (fig. 451). The stalk cell is sterile and produces nothing ; but the body cell enlarges (fig. 452), and there appear within it, near the nucleus, two remarkable bodies, the *blepharoplasts*. The body cell then divides to form the two *sperm mother* cells (fig. 453), in each of which is one of the blepharoplasts. In

a Cuban cycad (*Microcycas*) recently studied, as many as sixteen mother cells and sperms have been found in a single pollen tube. Within each mother cell a large, spirally grooved, multiciliate sperm is formed (figs. 453, 454), which is discharged and swims freely (figs. 455, 456). The blepharoplast has received its name from the fact that it develops the cilia. The discovery of these swimming sperms of Cycadales was quite unexpected, since it had been supposed that all seed plants had abandoned swimming sperms ; but the discovery served to emphasize the fern connections of the cycads.

Fertilization. — The pollen tube penetrates the tissue of the nucellus in various directions, often branching, and always functioning as an absorptive structure (*haustorium*). Finally it collapses, and the tube nucleus may return to the grain end of the tube. In the meantime the tissue of the nucellus lying between the pollen chamber and the archegonial chamber has broken down, and the two chambers become continuous. Then the sperms are discharged into the archegonial chamber, and finding their way into the archegonium fertilize the egg. It is evident that the pollen tube in these primitive seed plants is not a means of

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FIG. 459. — Differentiation of proembryo of *Zamia* by elongation of cells of suspensor region; unelongated cells above suspensor forming the "rosette"; apical group of small meristematic cells (note spindles) to form the embryo. — After COULTER and CHAMBERLAIN.

carrying the sperms to the archegonia, but is simply an absorptive organ.

Embryo. — The development of the embryo differs in detail among the cycads, but the general features are fairly constant (figs. 457, 458). The first stage is that of free nuclear division, resulting in a distribution of nuclei through the cytoplasm of the huge egg (fig. 457). For example, in *Zamia* there are eight successive divisions, resulting in 256 free nuclei. The next stage is that of wall formation, which varies in extent, sometimes resulting in a tissue which nearly fills the egg, but sometimes (as in *Zamia*) being restricted to the lower region of the egg (fig. 458). This tissue, which in *Zamia* occupies the lower end of the egg, is the *proembryo*. The cells behind the tip cells of the proembryo begin to elongate remarkably (fig. 459), forcing the tip cells out of the archegonium into the nutritive tissue of the gametophyte (*endosperm*), and continue to elongate until they form an exceedingly long, tortuous, and often spirally coiled massive filament (*suspensor*), sometimes 5 cm. or more long (fig. 460). The tip cells at the end of this long suspensor form the embryo, which develops two cotyledons, a constant feature of cycads. In the germination of the seed these cotyledons remain within the testa.

FIG. 460. — Embryo of *Cycas circinalis*, showing (above) the remains of proembryonic tissue, the long and coiled suspensor, and the terminal embryo. — After TREUB.

Changes in terminology. — In passing from pteridophytes to spermatophytes, it is sometimes confusing to the beginner to fit the older terminology of the seed plants to the more recent terminology of the lower groups. It is important that this change in terms should not give rise to the idea that there is any change in the character of the structures. The following list should prevent any possibility of confusion in this transition from one set of terms to another. The real name of the structure, as used in the lower groups, is followed in each case by the older name applied in seed plants before any such relationship was known: microsporophyll (stamen), megasporophyll (carpel), microsporangium (pollen sac), megasporangium (ovule), microspore (pollen grain), megaspore (embryo sac), female gametophyte (endosperm).

Conclusions. — The fernlike characters of the cycads appear in the vascular anatomy, mesarch and even concentric bundles still being pres-

ent ; in the form and general character of the leaves ; in the microsporophylls with their abaxial sporangia in sori ; and in the swimming sperms. These characters are shared with Cycadofilicales and Bennettitales, the ovules of which groups those of cycads further resemble in the three-layered testa (the outer and inner layers fleshy and the middle one stony), the two sets of vascular strands, and the nucellar beak with its pollen chamber. The general habit of the sporophyte body further resembles that of the Bennettitales ; but the relatively terminal and monosporangiate strobili are peculiar to cycads.

The cycads evidently represent the modern end of one seed plant line, which has come from the fernlike Cycadofilicales of the Paleozoic, and which gave rise to the Bennettitales during the Mesozoic.

(4) Cordaitales

General character. — This is an extinct paleozoic group of gymnosperms that was contemporary with the Cycadofilicales, and these two groups made up most of the seed plant vegetation of the Paleozoic, the Cordaitales being the dominant gymnosperm forest type. The two groups appear side by side as far back as the records go, but intergrading forms indicate that the Cordaitales probably arose from the Cycadofilicales at a very early period.

Sporophyte. — The Cordaitales were tall and slender trees, often 10 to 30 m. high before branching, with a dense crown of branches, and a great abundance of simple and large leaves (fig. 461). The general appearance of these trees differs from that of any living gymnosperm.

Vascular anatomy. — The structure of the stem combines the characters of other groups and suggests its relationships. The siphonostele composed of collateral endarch vascular bundles is common to all gymnosperms ; the mesarch bundles of the leaves, a character shared with the gymnosperm line beginning with Cycadofilicales and ending with Cycadales, testifies to the connection with ferns ; the large pith is shared with the same gymnosperm line ; the double leaf trace is also a feature of the Cycadofilicales; but the branching habit, the simple leaves, and especially the thick cylinder of secondary wood are characters of the Coniferales. These characters indicate a connection with the Cycadofilicales, and a development towards the Coniferales instead of towards the Cycadales.

Leaves. — The leaves are simple, elongated (fig. 461), with parallel

veins that branch dichotomously, except in certain forms with very narrow leaves. In some forms the leaves are short and obovate, suggesting those of Ginkgoales. The structure of the leaves is like those of the cycads, with the very characteristic mesophyll (see p. 193). In form, therefore, the leaves in general resemble those of the conifers; but in structure they resemble those of the cycad line.

FIG. 461. — Restoration of *Dorycordaites*, one of the Cordaitales, showing the branching habit, the simple, elongated, parallel-veined leaves, and the clusters of strobili borne on lateral branches. — After GRAND'EURY.

Strobili. — The strobili are small and monosporangiate, both kinds of strobili usually occurring on the same plant (monoecious), characters which belong to the conifers. They occur in clusters on lateral branches (fig. 461), and both kinds are sheathed by bracts.

Staminate. — The staminate strobilus is made up of spirally arranged sterile bracts, among which the stamens occur, either solitary or grouped near the apex (fig. 462). Each stamen is a slender stalk bearing a terminal cluster of three to six erect sporangia with longitudinal dehiscence. It is only among the Cycadofilicales that such terminal and erect microsporangia are found (cupule type, see p. 184).

Ovulate. — The ovulate strobilus is made up of conspicuous overlapping bracts, in whose axils short branches appear, each of which

bears one or two bractlets and a terminal ovule (fig. 463). The bearing of ovules on secondary axes of the strobilus results in what is called a *compound strobilus*, a type of strobilus characteristic of certain conifers.

Ovules. — Although the structure of the testa is not clear in the sections that have been made (fig. 463), two layers are evident (the outer fleshy and the stony), and it is probable that an inner fleshy layer was also present. This type of testa is characteristic of the whole cycad line of gymnosperms. Another primitive feature of the ovule is that the nucellus is quite free from the integument, and that one of the sets of vascular strands traverses the outer fleshy layer, and the other set traverses the peripheral region of the nucellus. This structure is duplicated only among the Cycadofilicales. There is also a prominent nucellar beak and a large pollen chamber, a structure which indicates the existence of swimming sperms.

FIG. 462. — Section of staminate strobilus of one of the Cordaitales, showing the spirally arranged sterile bracts, and the stalked stamens bearing terminal sporangia (the longitudinal dehiscence of the sporangia not shown). — After RENAULT.

Male gametophyte. — The pollen grains are preserved in abundance, and in favorable specimens a group of internal cells is evident (fig. 464), which must represent a male gametophyte; but whether these cells are vegetative or spermatogenous or both cannot be determined. In either case, the number of cells indicates a very primitive condition.

Female gametophyte. — The female gametophytes resemble those of modern gymnosperms. Two archegonia have been seen, and between

them a beaklike projection of the endosperm, a structure that characterizes *Ginkgo*. No seeds have been found containing embryos; and since the same fact is true of the Cycadofilicales, it is evident that all the seed plants of the Paleozoic shared this peculiarity.

FIG. 463. — Section of ovulate strobilus of one of the Cordaitales, showing the large overlapping bracts, in the axils of two of which there appear short branches bearing terminal ovules; that to right also shows a bractlet. — After RENAULT.

Conclusions. — A summary of the characters of Cordaitales shows an interesting combination. There are primitive characters which indicate connection with the Cycadofilicales and the cycad line, such as the large pith, the structure and mesarch bundles of the leaf, the structure of the ovule, and the swimming sperms. The advanced characters are the lofty and branching habit, the thick cylinder of secondary wood, the form of the leaves, and the compound ovulate strobilus, all of which are characters of the Coniferales. It

FIG. 464. — Pollen grains of one of the Cordaitales, showing the group of internal cells that probably belong to the male gametophyte. — After RENAULT.

seems evident, therefore, that the Cordaitales represent a second great branch from the Cycadofilicales stock, a branch which leads towards the Coniferales. This branch seems to have separated from the Cycadofilicales long before the other branch which ends in the modern Cycadales.

(5) Ginkgoales

General character. — *Ginkgo biloba*, the maidenhair tree, is the only living representative of a gymnosperm line that reaches back to the paleozoic Cordaitales, and was most extensively displayed during the Mesozoic. Its extensive cultivation by the Chinese and the Japanese, especially in temple grounds, first brought it into notice, and for a long time it was supposed that it did not exist in the wild state. In recent years, however, it has been found growing wild in the mountains of western China.

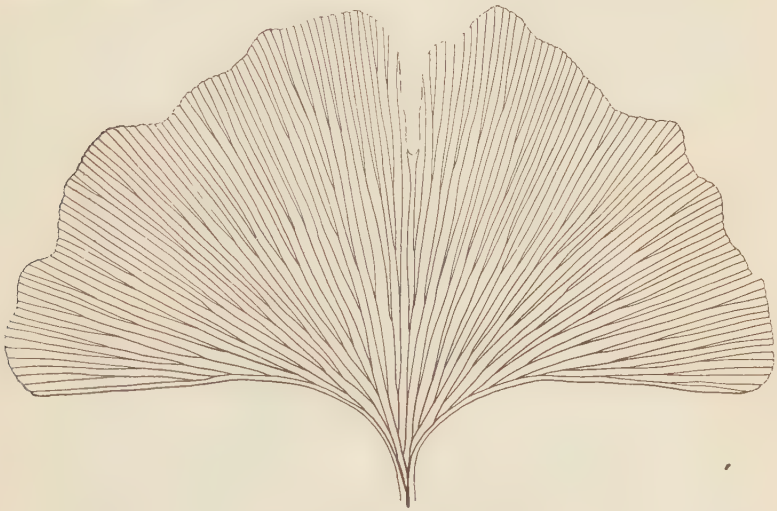


Fig. 465. — The leaf of *Ginkgo*.

Sporophyte. — *Ginkgo* is a tree with the general habit of a conifer, and therefore very unlike a cycad. As in both Cordaitales and Coniferales, it develops two kinds of branches: long shoots bearing scattered foliage leaves, and dwarf shoots bearing a few crowded leaves.

Vascular anatomy. — The anatomy of the stem closely resembles that of the Coniferales, with its thick cylinder of secondary wood and its relatively small pith, the latter character contrasting with the large pith of Cordaitales. All traces of mesarch bundles have disappeared from the stem, and also from the leaves, but they occur in the cotyledons. It is evident that in vascular anatomy *Ginkgo* has departed farther from the ferns than have the Cordaitales or the cycad line.

Leaves. — The leaf is very characteristic in form and venation (fig. 465), the broadly wedge-shaped outline, often more or less lobed, and the forked veins resembling somewhat the leaves of maidenhair fern and suggesting the common name. The mesophyll has the peculiar character (transversely elongated and very loosely arranged cells) described under Cordaitales and Cycadales (p. 193).

FIGS. 466, 467. — Staminate strobilus of *Ginkgo:* 466, the clusters of strobili borne on dwarf branches; 467, a single strobilus, showing the character of the individual stamens (a stalk ending in a knob and bearing two pendent sporangia).

Strobili. — The strobili are monosporangiate, and the two kinds of strobili occur on different trees (dioecious).

Staminate. — The staminate strobili occur in loose catkin-like clusters borne on the dwarf branches (fig. 466). The sporophyll (stamen) consists of a stalk ending in a knob, from beneath one side of which two (sometimes three to seven) pendent sporangia are borne (fig. 467). This type of stamen suggests the epaulet type found among Cycadofilicales (see p. 184). The development of the sporangium is regularly eusporangiate, as described under Cycadales (p. 194).

Ovulate. — The ovulate strobili are also borne on the dwarf branches and are very much reduced (fig. 468). A strobilus consists of a long stalk, near the tip of which usually two ovules are borne, only one of which usually matures a seed (fig. 469). At the base of each ovule there is a little cupule or *collar*, which is the rudiment of the sporophyll (fig. 470). Sometimes there are three or four ovules on a strobilus, and sometimes the collar becomes leaflike; so it is evident that the strobilus is remarkably reduced, usually producing only two ovules upon very rudimentary sporophylls.

FIG. 468. — Ovulate strobili of *Ginkgo*, borne in clusters on dwarf branches, and each bearing two ovules.

Ovules. — The ovules resemble in general structure those of Cordaitales and the cycad line already described (fig. 470), with the three-layered integument (outer fleshy, stony, and inner fleshy layers), the nucellar beak, and the pollen chamber; but the set of vascular strands, which in the groups referred to traverse the outer fleshy layer, are not present in *Ginkgo*, only the inner set appearing in the inner fleshy layer.

FIG. 469. — Ovulate strobili of *Ginkgo* bearing developing seeds; the strobili to the right have developed single seeds; those to the left have developed both seeds.

The megaspore mother cell is first observed deep within the nucellus, and it becomes invested by a distinct zone of glandular tissue. This glandular zone is digestive in function, invading and destroying the surrounding tissue of the nucellus. Surround-

ing the mother cell, therefore, there are three distinct concentric zones of tissue: (1) the invading digestive zone; (2) the invaded and disorganizing zone; and (3) the storage zone, outside of the disorganizing zone, and containing food surplus in the form of starch. After the female gametophyte (endosperm) is organized, it in turn invades and destroys the digestive zone and all the surrounding tissues of the nucellus. The mother cell forms the usual linear tetrad of megaspores, only the innermost one enlarging and functioning.

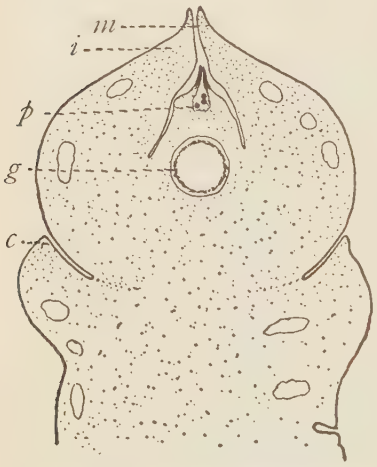


FIG. 470. — Section of ovule of *Ginkgo*, showing thick integument (*i*), micropyle (*m*), nucellar beak with pollen chamber (*p*), collar (*c*), and young female gametophyte (*g*). — After COULTER and CHAMBERLAIN.

Female gametophyte. — The female gametophyte develops as described for Cycadales (see p. 196), with free nuclear division (up to 256 free nuclei), parietal tissue (fig. 470, *g*), and centripetal growth. It is a remarkable fact that this female gametophyte becomes green, although enclosed within a three-layered testa, one layer being thick and fleshy and another compact and stony. The gametophyte continues its growth until it destroys all the nucellar tissues and reaches the testa.

Archegonia. — The archegonia are usually two in number (sometimes three), and develop as described for the cycads, including the organization of the archegonial jacket (see p. 197). In cycads a ventral nucleus is formed and speedily disorganizes, but in *Ginkgo* a cell wall is developed separating the ventral nucleus from the egg, so that there is a ventral canal cell, a feature which persists in some of the conifers. In *Ginkgo* the archegonial chamber is formed as usual, but between the two archegonia the endosperm grows into a conspicuous central beak, which reduces the archegonial chamber to a circular crevice (fig. 471). This peculiar feature appears also in the Cordaitales, but is not known in any other group of gymnosperms.

Male gametophyte. — The male gametophyte develops two vegetative cells (the first one lasting only until shedding, the second one persist-

ing), a generative cell, and a tube nucleus. This is the shedding stage, and the subsequent development occurs in the pollen chamber, after the pollen tube has begun to develop. In that position the nucleus of the generative cell divides, but no wall is formed, the stalk nucleus being thrust out to one side of the general cytoplasm, which organizes the body cell in connection with the other nucleus. The events that follow are exactly as in the cycads: two blepharoplasts appearing in the body cell; the body cell dividing into two sperm mother cells, each

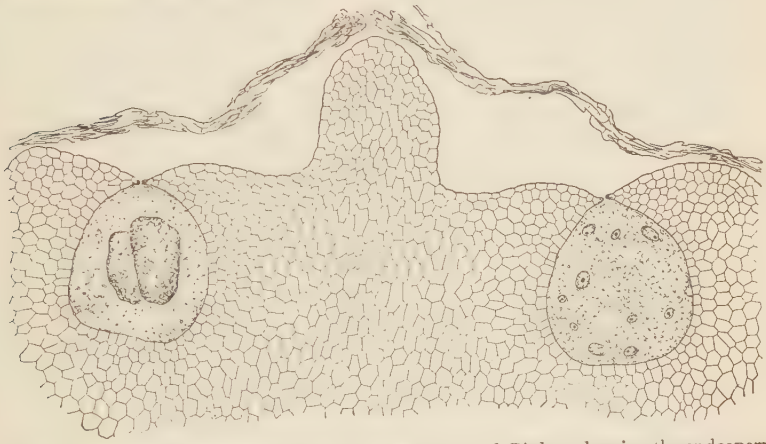


Fig. 471. — Micropylar end of female gametophyte of *Ginkgo*, showing the endosperm beak developed in the archegonial chamber, and the two archegonia; in the left archegonium the sperm and egg nuclei are fusing; in the right archegonium the early free nuclear division of the embryo is occurring.

with one blepharoplast; and each mother cell developing a spirally grooved, multiciliate sperm, which later is discharged.

Fertilization. — The details of fertilization also resemble those in the cycads. The pollen tube is a branching and absorptive (haustorial) organ; the pollen chamber and archegonial chamber become continuous by the breaking down of the small amount of intervening tissue; the grain end of the tube is thus brought into position favorable for the discharge of sperms into the archegonial chamber; and fertilization is accomplished (fig. 471).

Embryo. — The embryo is peculiar among gymnosperms in the absence of a slender, elongated, and tortuous suspensor, but a real suspensor is present. Free nuclear division (fig. 471) results in the distribution of 256 nuclei through the cytoplasm of the egg, and then walls

form, filling the egg with tissue (proembryo) more completely and permanently than in any other known gymnosperm (fig. 472). The cells of the upper two thirds of this proembryo remain inactive; while the cells of the lower third (which are much smaller) grow actively, forming a broad cylinder that invades the endosperm. This cylinder is really a massive suspensor, and at its tip the embryo is formed. This embryo, as in cycads, has two cotyledons, but sometimes three have been observed, and they also remain in the seed during germination.

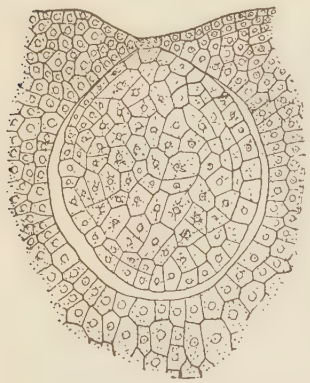


FIG. 472. — Proembryo of *Ginkgo*, filling the egg with tissue. — After STRASBURGER.

Conclusions. — *Ginkgo* resembles the Cordaitales and the cycad line in the structure of its ovules, and in its swimming sperms; but it is like the conifers in the habit of its sporophyte body and in its stem structure. Its origin from the Cordaitales seems clear, but the primitive reproductive characters which persist also distinguish it from Coniferales as a separate line.

(6) CONIFERALES

General character. — This is the large group of living gymnosperms, comprising approximately 350 recognized species, included in forty genera. In contrast with the tropical distribution of the cycads, the conifers are characteristic of the north and south temperate zones. Two families are recognized: *Taxaceae*, in general with fleshy seeds and freely exposed ovules; and *Pinaceae*, in general with dry seeds and ovules covered by scales. The Taxaceae comprise about eleven genera and 100 species; while the Pinaceae comprise about twenty-nine genera and 250 species. The two families differ so much that they must be treated separately.

(a) Taxaceae

General character. — The Taxaceae comprise two well-marked tribes or subfamilies: *Podocarpineae* (the podocarps) and *Taxineae* (the taxads). The podocarps in general are south temperate, *Podocarpus* being the largest genus (about sixty-five species), and as characteristic

of the southern hemisphere as are the pines of the northern hemisphere. The taxads in general are north temperate, *Taxus* (yew) being the most widely distributed genus.

Sporophyte. — The habit of the sporophyte body is familiar, in general being the branching habit established in *Ginkgo* and common to all conifers. In size the body ranges from large trees to straggling bushes. The mesarch type of bundle, characteristic of ferns, occurs in the stem of at least one species (a *Cephalotaxus*), but in most of them it is found only in the cotyledons, as in *Ginkgo*. The leaves are entire, as in all conifers, and range in breadth from the needles of *Taxus* to the broad blades of certain species of *Podocarpus*.

Staminate strobilus. — The staminate strobilus is always a distinct strobilus, enveloped by sterile bracts (as among Cordaitales, fig. 473). The sporophylls differ in form in the two tribes. Among the podocarps the sporophyll is bractlike, with two abaxial sporangia and a sterile tip (fig. 474); while among the taxads the sporophyll is peltate (epaulet type), as in *Ginkgo*, and bears a variable number of pendent sporangia (figs. 475, 476). The development of the microsporangium is as usual among eusporangiates. The microspores (pollen grains) of the podocarps are peculiar in being winged, each pollen grain developing two winglike extensions from the exine, as among the pines.

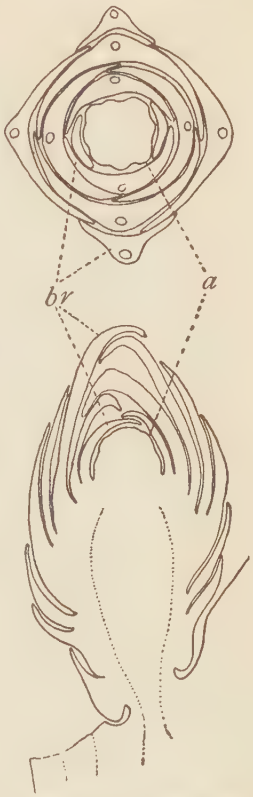


FIG. 473. — Cross and longitudinal sections of young staminate strobilus of *Torreya*, showing the overlapping bracts (*br*) and the position of the developing stamens (*a*). — After COULTER and LAND.

Ovulate strobilus. — The ovulate strobilus is much reduced, usually containing a single terminal ovule. For example, in *Torreya* (nearly related to *Taxus*) the ovulate strobilus resembles a simple ovulate flower, with four bracts (two decussate pairs) investing a terminal ovule (fig. 477).

Ovule. — The integument of the ovule is of the ancient type, developing three distinct layers (outer fleshy, stony, and inner fleshy); and a set of vascular strands traverses the outer fleshy layer, the inner set

FIGS. 474–476. — Microsporophylls (stamens) of Taxaceae: 474, *Podocarpus* (after HOOKER); 475, *Taxus* (after RICHARD); 476, *Torreya* (after HOOKER). — From ENGLER and PRANTL.

free from the integument, but as the ovule develops largely from beneath, the region in which the nucellus and integument are free from one another is carried to the tip of the ovule. A notable change in the ovule, as contrasted with the preceding groups of gymnosperms, is that there is no nucellar beak or pollen chamber (fig. 477); nor is there developed about the megaspore mother cell any special digestive (glandular) zone of cells, as in *Ginkgo*. The development of the linear tetrad and the selection of the innermost megaspore for functioning are as usual.

Female gametophyte. — The female gametophyte develops by the usual stages: free nuclear division (up to 256 nuclei), parietal wall formation, and centripetal growth. It is important to note the variation in the appearance of the archegonial initials. In some cases they are not differentiated until the gametophyte has become quite extensive; that is, they appear comparatively late in its history. In other cases, however, notably in *Torreya*, the archegonium initials appear as soon as wall formation has filled the embryo sac with tissue (figs. 478, 479).

Archegonia. — The archegonia range in number from one to eleven, the neck (belonging to the inner fleshy layer) being suppressed. This is just the reverse of the vascular condition in *Ginkgo*, in which the set of vascular strands belonging to the outer fleshy layer is suppressed, and the set belonging to the inner fleshy layer is developed. In early stages of the ovule the nucleus is entirely

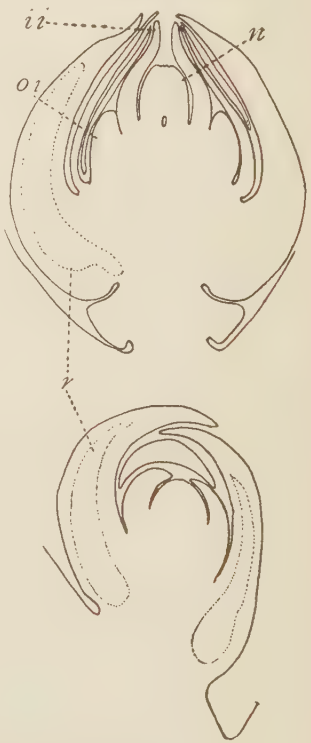


FIG. 477. — Longitudinal sections of ovulate strobilus of *Torreya* at different ages, showing the enveloping bracts and the solitary terminal ovule; upper section (the older) shows the two integuments (*ii*, *oi*), nucellus (*n*), and deep-placed mother cell. — After COULTER and LAND.

consisting usually of two (fig. 478) or three cells, but in *Podocarpus* it sometimes becomes a massive structure of about twenty-five cells. There is no well-defined archegonial jacket, and when it is remembered that there is no special digestive zone about the mother cell, it is evident that the nutritive mechanism is not differentiated in this group as it is in *Ginkgo*, or even in the cycads. In the division of the nucleus of the ventral cell, which precedes the formation of the egg, there is no separating wall formed, and hence no ventral canal cell. The ventral nucleus is its only representative, and in *Torreya* it is doubtful whether even this appears. The disappearance of the ventral canal cell and its nucleus is the last stage in the reduction of the axial row, which thereafter is represented only by the egg.

FIG. 478. — Young archegonium of *Torreya*, showing the two neck cells and the central cell. — After COULTER and LAND.

Male gametophyte. — In the development of the male gametophyte, the podocarps and taxads show a striking contrast. In the podocarps two to six vegetative (prothallial) cells appear (fig. 480); while in the taxads no vegetative cells have been discovered. The division of the generative (primary spermatogenous) cell into the sterile stalk cell and the body cell is as described for the preceding groups (fig. 480); but a striking change appears in the fact that there are no blepharoplasts in the mother cell, which means that ciliated (hence swimming) sperms are not formed. The nucleus of the body cell divides, and this division may be accompanied by a separating wall, so that two sperm mother cells are formed (taxads); or the nuclear division may not be accompanied by wall formation, so that there are only two mother cell nuclei in the general cytoplasm of the body cell (podocarps). In either case the division is unequal, so that only one cell or one nucleus functions (fig. 479). No sperms are formed, but the mother cell functions directly as a sperm, its nucleus being the structure essential in fertilization. It has become the habit to call these mother cells that do not form sperms internally and discharge them, but function themselves as sperms, simply *male cells*.

Fertilization. — In pollination (by the wind) the pollen grains come to rest on the tip of the nucellus, and in the absence of a pollen chamber

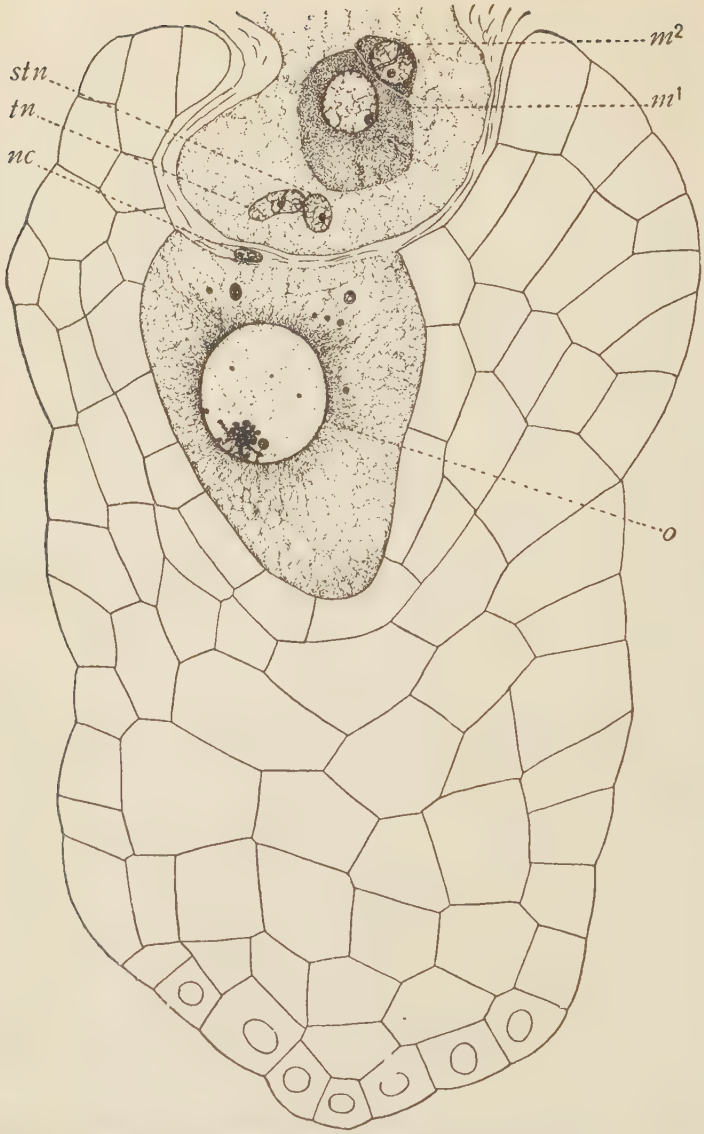


FIG. 479. — Mature female gametophyte of *Torreya*, showing the single archegonium containing a large egg nucleus (*o*), remnants of the neck canal cell nucleus (*nc*), and the tip of the pollen tube containing tube nucleus (*tn*), stalk cell nucleus (*stn*), and the two unequal male cells (m^1, m^2). — After COULTER and LAND.

there is much nucellar tissue to be traversed before the female gametophyte with its archegonia is reached. For the first time, the pollen tube acts as a carrier of the male cells, the body cell, which is to divide, entering the tube and remaining near its tip as it advances through the tip of the nucellus (fig. 479). The tube may advance directly towards the archegonia or it may pursue a devious route, in some cases not reaching the archegonia until during the second season. When an archegonium is reached, its neck is broken through and the contents of the tip of the pollen tube are discharged into the egg (fig. 481).

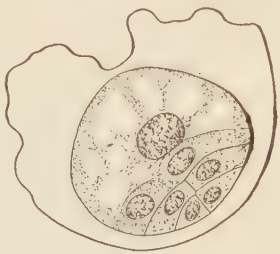
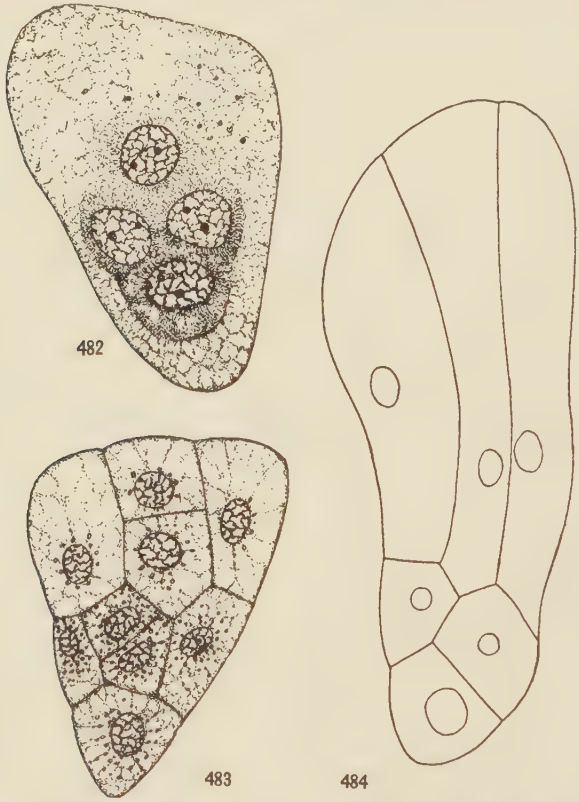


FIG. 480. — Male gametophyte of *Dacrydium* (one of the podocarps) at shedding stage of pollen, showing four vegetative cells, stalk and body cells (formed by the generative cell), and the tube nucleus. — After MISS YOUNG.

Embryo. — In the development of the embryo from the fertilized egg, there is a variable amount of free nuclear division, from four free nuclei (*Torreya*, fig. 482) up to thirty-two, in strong contrast with the very numerous free nuclei appearing in the embryogeny of cycads and of *Ginkgo*. After the free nuclei are formed, walls appear, and the resulting tissue (proembryo) fills the egg. In general, there are about three tiers of cells in the proembryo, the lowest (innermost) one usually consisting of a single cell, so that the proembryo has a general conical outline (fig. 483). An elongation of cells begins in the upper (outermost) tier (fig. 484), and this is continued by the middle tier, so that the terminal cell, which is to form the embryo, is thrust out of the archegonium and

FIG. 481. — Fertilization of *Torreya:* the pollen tube has discharged its contents into the egg, and the male and female nuclei are fusing. — After COULTER and LAND.

deep into the endosperm by the rapidly and extensively elongating suspensor. In the organization of the embryo two cotyledons appear, as in all the preceding groups of gymnosperms. *Torreya* is peculiar in the irregular growth of its endosperm (female gametophyte), which



FIGS. 482–484. — Embryo of *Torreya:* 482, the stage of four free nuclei; 483, the completed proembryo (filling the egg), the cells approximately in three tiers; 484, uppermost tier of proembryo elongating to form suspensor. — After COULTER and LAND.

encroaches upon the surrounding nucellar tissue in such a jagged way as to give the appearance in the seed called *rumination*, which may be seen also in sections of nutmegs.

Conclusions. — The Taxaceae have not been traced with certainty below the middle of the Mesozoic, so that it seems to be a comparatively modern group among gymnosperms. It has made a decided advance

beyond the groups previously considered in the loss of swimming sperms and the related structures of the ovules, and also in other features; nevertheless, it has also retained certain primitive features, as, for example, the presence of mesarch bundles in the cotyledons and even in the stem. The general relationships of the family will be considered in connection with the Pinaceae.

(b) Pinaceae

General character. — This family, characterized in general by its conelike ovulate strobili and dry seeds, includes the conspicuous

FIG. 485. — Transverse section of a three-year-old twig of *Pinus sylvestris*, showing the small pith, the thick and compact vascular cylinder of secondary wood, and the cortex; radiating lines through the wood represent the narrow pith rays; resin ducts in both wood (small) and cortex (large); to the right is a branch gap in the cylinder.

gymnosperm vegetation of north temperate regions. Four tribes are recognized, as follows:

Abietineae (9 genera and about 140 species), including pines, spruces, firs, hemlocks, larches, and cedars, the large genus being *Pinus*, with about 80 species.

Taxodineae (8 genera and about 15 species), including the characteristic American genera *Sequoia* (redwood) and *Taxodium* (bald cypress).

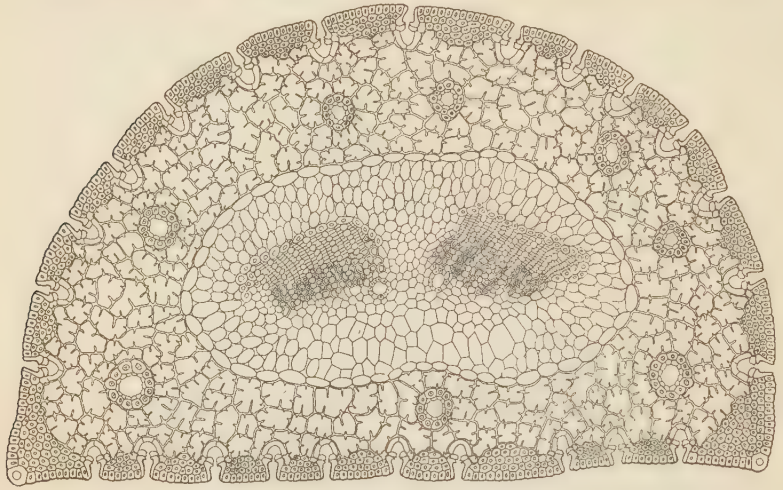
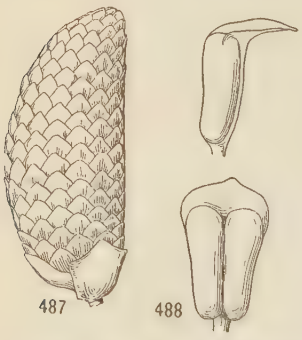


FIG. 486. — Transverse section of a pine needle, showing the epidermis (in which are deeply sunken stomata) underlaid by several layers of heavy-walled cells (sclerenchyma), the mesophyll with characteristic infolded walls and containing resin ducts, the distinct bundle sheath (endodermis) surrounding the vascular region (stele), and the two parallel vascular bundles (xylem directed towards the flat face of the leaf).

Cupressineae (9 genera and about 80 species), including the cypress, arbor vitae (false cedar), and junipers, the large genus being *Juniperus*, with about 30 species. This tribe is peculiar among Coniferales in its opposite (cyclic) leaves.



487 488

FIGS. 487, 488. — Staminate cone (487) and microsporophylls (488) of pine (the latter in two views), showing the two abaxial sporangia and the sterile tip.

Araucarineae (2 genera and about 20 species), known as araucarians or araucarian pines, and characteristic of the southern hemisphere.

Sporophyte. — The general habit of the sporophyte body is sufficiently indicated by the familiar forms mentioned above (also see fig. 955). The vascular cylinder, with its endarch bundles, its thick cylinder of secondary wood composed of radially arranged tracheids with bordered pits, is well known (fig. 485). So far as known,

all traces of the mesarch structure have disappeared, even from the cotyledons. The leaves vary from narrow needles (fig. 486) to broad blades and concrescent disks. When the blades are broad, transversely elongated mesophyll cells appear.

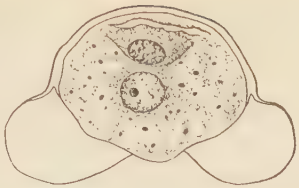


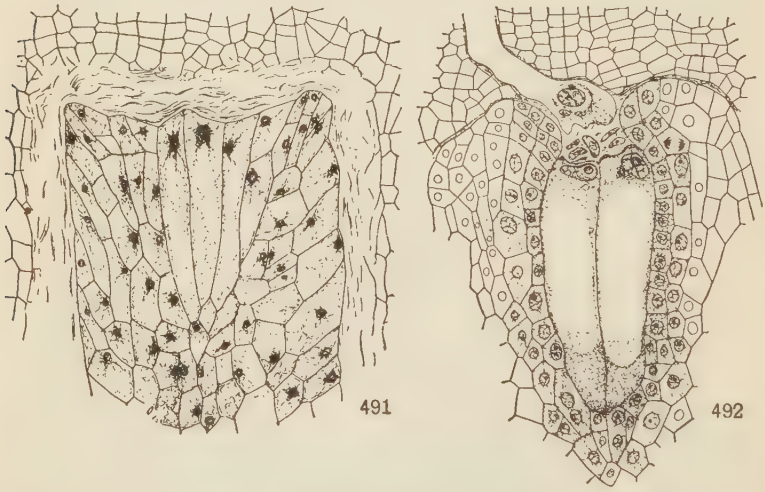
FIG. 489. — The winged and shedding pollen grain of pine, containing an early stage of the male gametophyte. — After COULTER and CHAMBERLAIN.

Staminate strobilus. — The staminate strobilus (fig. 487) is made up of sporophylls (stamens) which are exceedingly variable in form. In general, the stamen is bractlike, with sterile tip and abaxial sporangia (as in cycads and podocarps), the sporangia most frequently two in number (fig. 488), though sometimes more numerous; but in the araucarians

FIG. 490. — Various views of the ovuliferous scales and ovules of pine: on upper surface are borne two ovules (megasporangia) with micropyles directed towards the base of the scale; the seeds become winged by tissue developed from the scale.

the stamen is peltate (as in taxads), and one-sided peltate (as in *Torreya*). The sporangia are developed as usual, and in the Abietineae the pollen grains (microspores) are winged (as in podocarps, fig. 489).

Ovulate strobilus. — The ovulate strobilus of Pinaceae has been the subject of much discussion. In the Abietineae the strobilus is made up of a series of bracts, in the axil of each of which a so-called *ovuliferous scale* appears, which usually bears two ovules whose micropyles are directed towards the base of the scale (fig. 490). In the other tribes the bract and ovuliferous scale are more or less united. The discussion



FIGS. 491, 492. — Archegonium complex of *Thuja:* 491, group of archegonium initials; 492, two mature archegonia (reached by a pollen tube, in which the body cell has not yet divided) with a common archegonial chamber and a common archegonial (nutritive) jacket. — After LAND.

referred to has to do with the nature of the ovuliferous scale, and many facts indicate that it represents a fused pair of leaves of a dwarf axillary branch. This means that the ovules are borne in the strobilus on axes of the second order, as in Cordaitales, and that the ovulate strobilus of Pinaceae is a compound strobilus.

Ovule. — The structure of the ovule is as described for Taxaceae, except that the outer fleshy layer does not develop, and the seed is dry; that both sets of vascular strands have been eliminated; and also that there is the same elaborate nutritive mechanism that was described for *Ginkgo*. The development of the ovule and the seed is usually

a very prolonged process. Probably in no case is the period between the first appearance of the ovule and the shedding of the seed less than two growing seasons; and in some cases the seed is not shed until the third season after the ovule appears, pollination taking place during the second season.

Female gametophyte. — The development of the female gametophyte proceeds as in the previous groups, until an extensive endosperm is formed. At least two distinct regions of the endosperm are always evident; namely, a region of smaller cells towards the micropyle, in which the archegonia develop, and a deeper region of larger cells, which functions as a nutritive region.

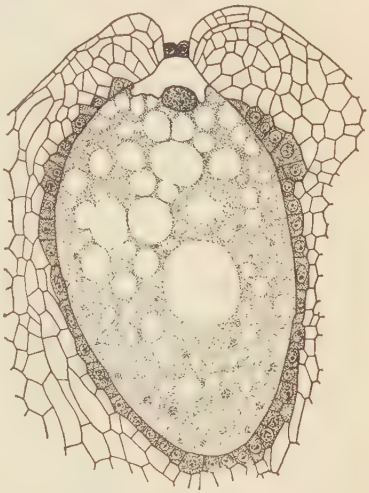
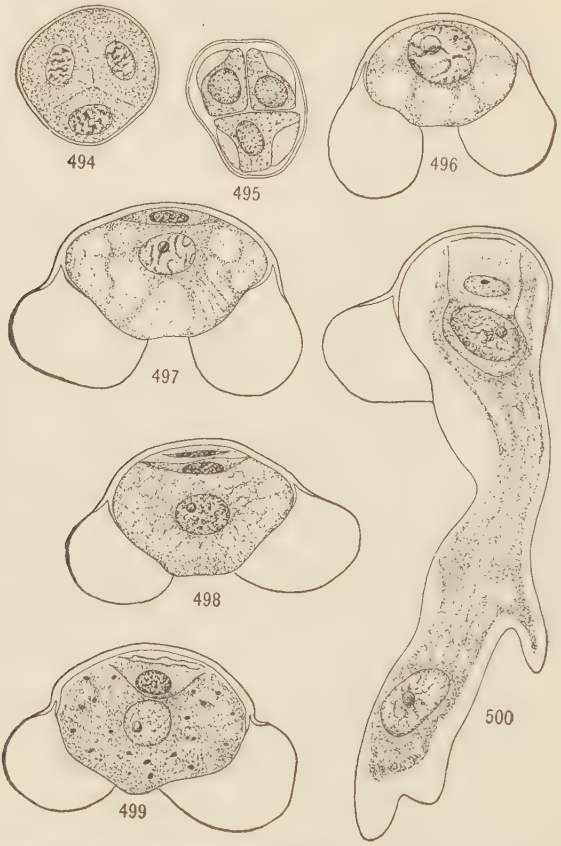


FIG. 493. — Archegonium of *Pinus*, showing two neck cells, the central cell (whose nucleus is just about to divide to form ventral canal and egg nuclei), and the archegonial jacket. — After COULTER and CHAMBERLAIN.

Archegonia. — The archegonia range in number from one to sixty, the usual numbers among the Abietineae being three to five. In the Taxodineae and Cupressineae an *archegonium complex* is organized; that is, a group of archegonia is invested by a common archegonial jacket and has a common archegonial chamber (figs. 491, 492). The necks of the archegonia are remarkably variable in the number of cells, ranging from the ordinary two-celled neck to that in *Pinus*, which consists usually of two tiers with four cells in each tier, but may reach four tiers with as many as sixteen cells in each tier. In the Abietineae a definite ventral canal cell is formed (fig. 493), but in Taxodineae and Cupressineae only a ventral nucleus appears (as in Taxaceae); while in Araucarineae the situation is unknown.

Male gametophyte. — The male gametophyte is quite variable as to the number of vegetative (prothallial) cells, but the condition is usually constant in each tribe. In Abietineae there are two vegetative cells, both of which are ephemeral (figs. 494–500); in Taxodineae and Cupressineae there are no vegetative cells (as in taxads); while in Arau-

carineae the vegetative cells are numerous (as in podocarps). As in Taxaceae, the generative cell divides into stalk and body cells, and the body cell passes into the pollen tube, where either it divides into two



FIGS. 494–500. — Male gametophyte of *Pinus:* 494, the forming tetrad of spores (pollen grains) within the mother cell; 495, young pollen grains forming wings; 496, a single mature pollen grain; 497, first vegetative cell cut off; 498, second vegetative cell cut off (first one disorganizing); 499, division to generative cell and tube nucleus (both vegetative cells disorganized) (shedding stage); 500, growth of the pollen tube, into which the tube nucleus has descended; division of generative cell into stalk (upper) and body cells. — After COULTER and CHAMBERLAIN.

cells (male cells), or its nucleus divides into two nuclei (male nuclei). The male cells in Abietineae are generally unequal, a condition apparently connected with the fact that only one functions; but in Taxodineae

and Cupressineae the male cells are equal, since both may function by the tube entering the chamber of an archegonium complex. The tip of the pollen tube, just before fertilization, contains the two male cells and also (usually in advance of them) the stalk and tube nuclei (fig. 501).

Fertilization. — The general features of fertilization are as described for the Taxaceae, the pollen tube acting as a carrier of the male cells to the archegonia, in addition to its old function as an haustorium.

Embryo. — In the development of the embryo (figs. 502–509), free nuclear division occurs until four to sixteen nuclei are formed, and sooner or later become placed at the bottom of the egg. With the next nuclear division walls appear, and division of cells continues until three or four tiers of cells are formed, the tiers containing approximately the same number of cells. This proembryo, therefore, by no means fills the cavity of the egg, as in the preceding groups of gymnosperms, the greater bulk of the egg being a large reservoir of surplus food material.

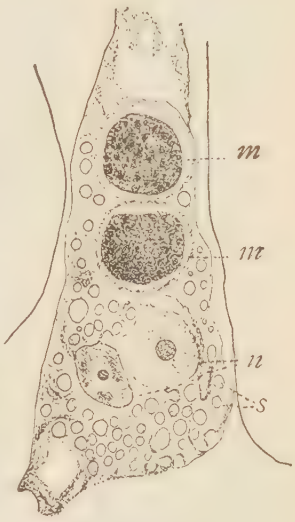
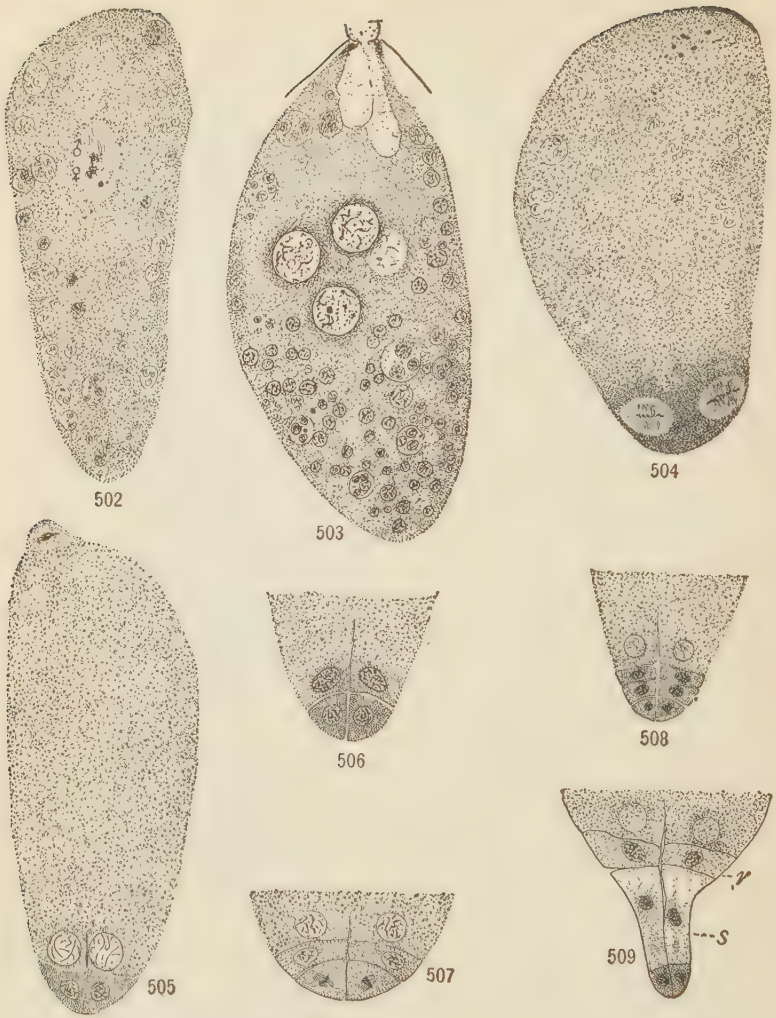


FIG. 501. — Tip of pollen tube of *Pinus*, just before fertilization, containing the two male cells (*m*), stalk and tube nuclei (*n*), and abundant starch grains (*s*). — After COULTER.

The proembryo of *Pinus* may be used to illustrate the general structure of the proembryo and the functions of its different regions (figs. 502–509). This proembryo is made up of four tiers of cells, with four cells in each tier. The uppermost tier consists of four cells, open (without walls) towards the food reservoir of the egg. The next tier, which is the part of the proembryo that remains within the egg, constitutes the so-called *rosette*. The third tier of four cells forms the suspensor, each cell elongating enormously, so that the four-celled suspensor becomes a long and tortuous filament. At the tip of the suspensor, thrust by its elongation deep into the endosperm, is the lowest tier of four cells, which forms the embryo (figs. 509, 510). All four of these cells may form one embryo, or each of the four cells may form a separate embryo. In any event, although several eggs may begin to form embryos, one embryo soon dominates and the others disappear.



FIGS. 502–509. — Development of embryo of *Pinus:* 502, fusion of male and female nuclei in the large egg; 503, four free nuclei (one in background) derived from fusion nucleus; 504, the four nuclei (two visible) at base of egg and dividing; 505, eight-nucleate stage (four nuclei visible); 506, the same a little further advanced; 507, next division, resulting in twelve cells in three tiers; 508, completed proembryo (four tiers of cells, uppermost open towards the general cytoplasm of the egg); 509, beginning of suspensor-formation (*s*), leaving within the egg the rosette cells (*r*), and thrusting out of it the four tip cells, which will form the embryo. — After COULTER and CHAMBERLAIN.

The cotyledons are not steadily two in number, as in the preceding groups of gymnosperms, but vary from two (mostly so in Cupressineae and Araucarineae) to as many as fifteen (in the Abietineae). It is because the pines and their allies are the most familiar gymnosperms that gymnosperms are commonly described as *polycotyledonous;* but it should be remembered that the occurrence of more than two cotyledons is a feature of only two tribes of Coniferales (Abietineae and Taxodineae), and that two cotyledons occur in some of the members even of these tribes.

FIG. 510. — Embryo of *Pinus*, showing (above) two cells of the rosette, two cells of the suspensor, and an early stage of the terminal embryo. — After COULTER and CHAMBERLAIN.

Conclusions. — It seems most reasonable to conclude that the Coniferales have been derived from the paleozoic Cordaitales, which also gave rise to the Ginkgoales. The Coniferales, however, have retained fewer primitive characters than the Ginkgoales, and are especially noteworthy in having lost the swimming sperms.

In comparing the six tribes of Coniferales, the testimony as to their relationships is very confusing. The testimony obtained from the geological record is necessarily incomplete, but so far as it is available the relative ages of the tribes are as follows: The Abietineae have been traced to the Paleozoic, and in all probability are the oldest of the Coniferales. The Araucarineae have been traced through the Mesozoic, in which period they were very abundant; and in all probability they are but little younger than the Abietineae. The Taxodineae and Cupressineae are recognizable in the Lower Mesozoic; while the Taxaceae (Podocarpineae and Taxineae) are not known below the middle Mesozoic. It may be that this sequence indicates the actual sequence of the tribes, but it is hard to reconcile it with the morphological characters detailed above. In any event, the fact that Coniferales as a whole have developed from the Cordaitales seems to be sufficiently clear, and is all that need concern the elementary student of the group. It should be remembered that origin from Cordaitales means also a connection through them with the ferns, and therefore that all gymnosperms have descended from ferns.

(7) Gnetales

General character. — This group comprises three very distinct genera: *Ephedra*, with about fifty species distributed throughout the arid regions of the Mediterranean basin and adjacent Asia, and also in the arid regions

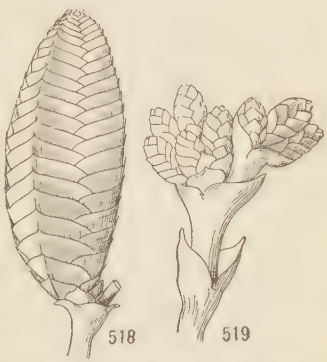
Figs. 511–516. — *Ephedra:* 511, branches bearing ovulate strobili; 512, branches bearing staminate strobili; 513, staminate strobilus, showing staminate "flowers" in axils of bracts; 514, ovulate strobilus; 515, an ovulate "flower"; 516, decussating bracts of the ovulate strobilus. — After Watson.

of western North America and South America; *Tumboa* (often called *Welwitschia*), represented by a single species in the arid districts of western South Africa; and *Gnetum*, with about fifteen species distrib-

uted throughout the tropics of both hemispheres. Gnetales have always attracted attention from the fact that in certain characters they resemble angiosperms more nearly than do the other gymnosperms.

FIG. 517. — *Tumboa*, showing the heavy conical body and the two-lobed crown bearing two broad parallel-veined leaves (in the photograph split into shreds) and strobilus-bearing branches.

Sporophyte. — The species of *Ephedra* are straggling shrubs, with long-jointed and fluted green stems, and scalelike opposite leaves forming at each joint a two-toothed sheath (figs. 511, 512, 975). *Tumboa* has a huge, woody, turnip-shaped body, whose crown bears a single pair of elongated, strap-shaped, parallel-veined, and persistent leaves (fig. 517). The species of *Gnetum* are small trees or woody twiners with leathery, net-veined, opposite leaves, resembling those of dicotyledons (fig. 522). It will be observed that a constant character of the group is the cyclic (opposite) leaves, a feature found among Coniferales only in the Cupressineae.



FIGS. 518, 519. — Ovulate (518) and staminate (519) strobili of *Tumboa*. — 518, after LE MAOUT and DECAISNE; 519, after HOOKER.

Vascular anatomy. — It is in their vascular anatomy that the Gnetales show a striking angiosperm character. The secondary wood does not consist exclusively of tracheids with bordered pits, as in the other gym-

nosperm groups, but in addition to these gymnosperm tracheids there are also true vessels of the angiosperm type.

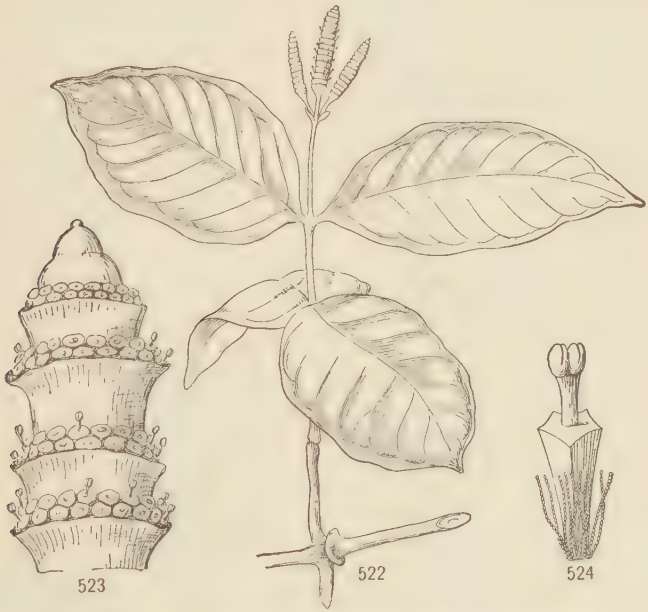
FIG. 520. — *Tumboa:* staminate "flower" (with bracts removed), showing the six trisporangiate stamens united below, and the sterile ovule with long and twisted micropylar tube. — Adapted from HOOKER.

Staminate strobili. — The staminate strobili are made up of pairs of decussate bracts, which are imbricate in *Ephedra* (fig. 513) and *Tumboa* (fig. 519), and connate in *Gnetum* (fig. 523). In the axils of these bracts are the so-called staminate flowers. In *Ephedra* and *Gnetum* a staminate flower consists of an axis bearing at its tip two or more sporangia (figs. 513, 524), and invested below by two or four bracts, which are free or coalescent in a tube. In *Tumboa* the structure is very different and quite remarkable. Within the investing bracts there is a whorl of six united (*monadelphous*) stamens, each of whose free tips bears three sporangia; and within the cycle of stamens there is a central (terminal) sterile ovule, whose remarkably long micropylar tube is spirally coiled and broadly flaring at the tip (fig. 520). This remarkable structure indicates that the ancestors of *Tumboa* had flowers that contained functioning stamens and ovules, and that in the case of *Tumboa* staminate and ovulate flowers arose by the disappearance of ovules in certain flowers, and of stamens in others. No such close association of stamens and ovules is known among gymnosperms, except in Bennettitales, where they occur in the same strobilus.

FIG. 521. — *Tumboa:* ovulate "flower," showing the enveloping and winged bracts, the two integuments (the inner forming the long micropylar tube), and the nucellus containing the embryo sac. — Adapted from STRASBURGER.

In attempting to interpret the staminate strobilus of the Gnetales, it is evident that the microsporangia are borne upon secondary axes (which are the so-called flowers), and therefore the strobilus is compound. In Cordaitales and in certain of the Coniferales there are compound ovulate strobili, but only in Gnetales do com-

pound staminate strobili occur. The bractlets of this secondary axis, which invest the stamens, were interpreted as representing the *perianth* of a flower, and the presence of a perianth was regarded as another striking angiosperm character of Gnetales; but if these bracts represent a perianth, those in the compound ovulate strobilus of Cordaitales also represent a perianth, as well as all bractlets on secondary axes of strobili. To extend the term *perianth* to include these vague conditions



FIGS. 522–524. — *Gnetum latifolium:* 522, branch bearing staminate strobili and the characteristic leaves; 523, part of staminate strobilus, showing the "connate" bracts, and in their axils numerous staminate "flowers"; 524, a single staminate "flower." — After BLUME.

is to make it difficult to define, and perhaps is to mislead as to the origin of the perianth of angiosperms.

Ovulate strobilus. — The ovulate strobili have the same general structure as the staminate, the so-called ovulate flowers arising in the axils of the bracts (figs. 514, 518, 526, 527). There is the same perianth structure observed in the staminate flowers, and in *Tumboa* there is said to appear outside of the ovule the rudiments of a stamen set.

FIGS. 525, 526. — *Gnetum latifolium:* 525, branches bearing ovulate strobili; 526, part of ovulate strobilus. — After BLUME.

of swimming sperms. In *Ephedra* a remarkable funnel-shaped pollen chamber is developed by the breaking down of the nucellar tissue (fig. 528), which extends to the embryo sac and exposes the necks of the archegonia; hence in pollination the pollen grains may come to rest in contact with the archegonium necks. In *Gnetum* the tip of the nucellus is more or less disorganized, and this is the only trace of a pollen chamber (fig. 530); while in *Tumboa* there is not even a trace.

Female gametophyte. — The structure of the female gametophyte in Gnetales is of great interest, for there is an evident approach towards the angiosperm condition.

Ovule. — The ovule has two integuments, the inner one forming a long tubular micropyle, which is a marked feature of the group (figs. 521, 528, 530). The nucellus has the usual gymnosperm feature of a heavy mass of sterile tissue overlying the megaspore mother cell (and later the embryo sac). In all the preceding groups of gymnosperms, except Coniferales, this overlying tissue is beaked and contains a pollen chamber, a structure associated with the presence

FIG. 527. — Ovulate strobili of *Gnetum*, with fleshy seeds maturing.

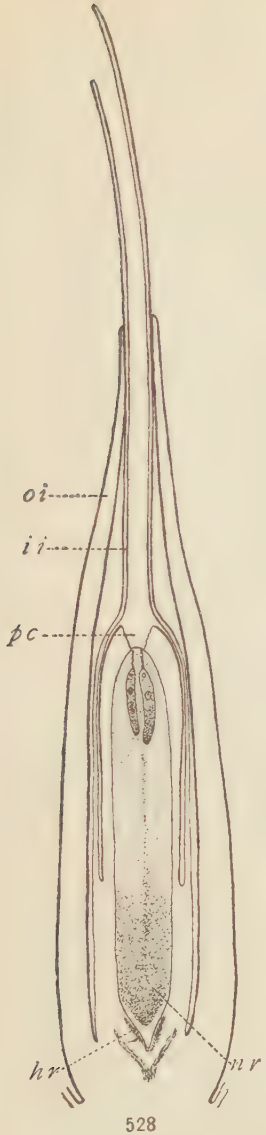


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FIG. 528. — Diagrammatic section of ovule of *Ephedra*, showing outer integument (*oi*), inner integument (*ii*) forming the long micropylar tube, the remarkable pollen-chamber (*pc*), and the elongated female gametophyte (within the embryo sac) with two long-necked archegonia. — After LAND.

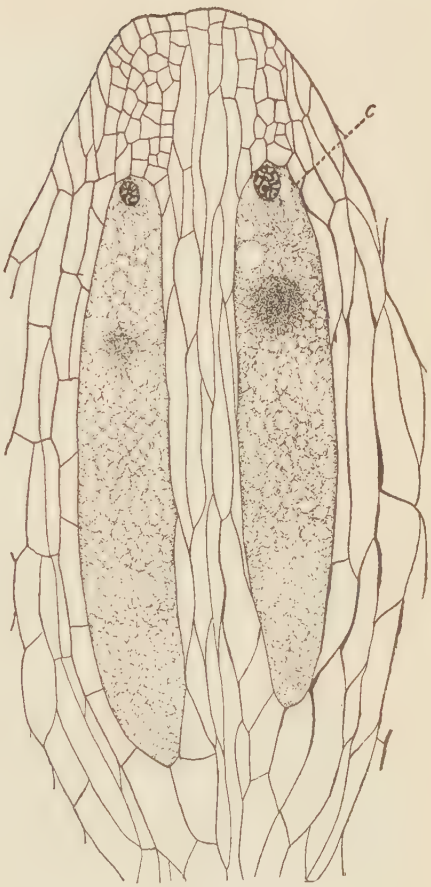
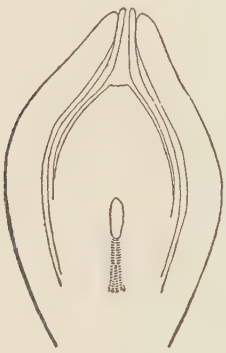


FIG. 529. — Archegonia of *Ephedra*, showing their elongated form and massive necks. — After LAND.

The three genera differ widely in this regard, and therefore must be considered separately.

Ephedra. — The female gametophyte is developed as in other gymnosperms, with free nuclear division (up to 256 nuclei), parietal wall formation, centripetal growth, and differentiation of the endosperm into distinct micropylar and antipodal regions. In this case, however, the antipodal tissue (nutritive) is relatively small-celled and compact, and the micropylar tissue is more loosely organized and has thinner walls. In this loose micropylar tissue usually two archegonia are formed, their very long, many-tiered necks extending to the pollen chamber described above (figs. 528, 529). In the organization of the egg, a ventral nucleus is cut off, and not a ventral cell.



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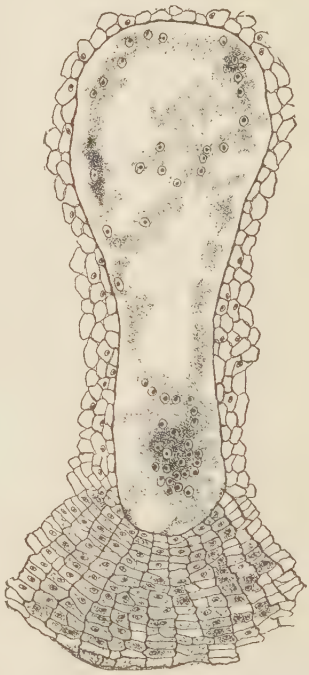

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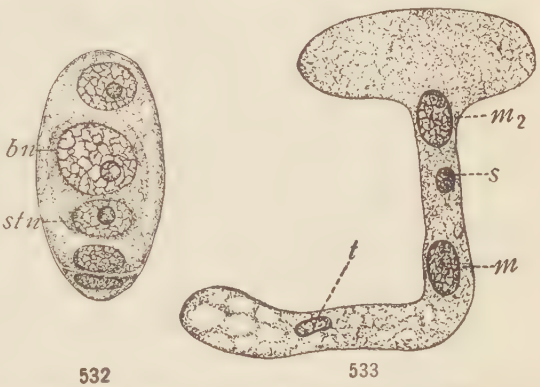
FIGS. 530, 531. — *Gnetum Gnemon:* 530, diagrammatic section of ovule, showing the two integuments (inner one forming the micropylar tube), nucellus with disorganized tip, and deep-placed embryo sac, beneath which is a mass of feeding (glandular) tissue; 531, enlarged view of same embryo sac (ready for fertilization), in which the female gametophyte consists of free nuclei (each a potential egg), and below which is the mass of feeding tissue. — After COULTER.

Tumboa. — The female gametophyte is developed as in *Ephedra* as far as wall formation; but in the differentiation of the endosperm into two regions (one fourth micropylar and three fourths antipodal) there is very incomplete wall formation. As a consequence, the cells of the

antipodal region are multinucleate, and those of the micropylar region become so (two to five-nucleate). Since there is no uninucleate cell in the micropylar tissue, there is no archegonium initial, and hence no archegonium. Instead, several of the multinucleate cells develop what have been called *prothallial tubes*, which penetrate the overlying nucellar tissue, and into them the nuclei pass, each nucleus being a potential egg nucleus. It is at this point that the archegonium disappears; which seems to be associated with the fact that the egg nuclei are differentiated before wall formation in the endosperm has been completed.

Gnetum. — In this genus there is free nuclear division as before, but wall formation does not occur, so that the embryo sac at the time of fertilization contains only free nuclei (fig. 531), and each one of these free nuclei is a potential egg nucleus. This is the general angiosperm condition. Below the antipodal end of the sac a remarkable nutritive (glandular) tissue is developed.



FIGS. 532, 533. — Male gametophyte of *Ephedra:* 532 pollen grain in shedding stage, containing two vegetative nuclei (below), stalk (*stn*) and body (*bn*) nuclei, and tube nucleus (above); 533, completed male gametophyte (after beginning of pollen tube), showing in the tube the male cells (*m*), stalk nucleus (*s*), and tube nucleus (*t*). — After LAND.

Male gametophyte. — The male gametophyte of Gnetales is known only in *Ephedra*. In its shedding condition the pollen grain of *Ephedra* contains two persistent vegetative cells, and conspicuous stalk, body, and tube nuclei (fig. 532). In this condition the pollen grain rests on the exposed archegonium necks, and before the pollen tube is formed the body nucleus divides into two equal male nuclei (fig. 533).

Fertilization. — The phenomena of fertilization vary with the structure of the female gametophyte. In *Ephedra* the pollen tube breaks through the long and massive neck of the archegonium (fig. 529); in *Tumboa* it comes into contact with the prothallial tubes that are pene-

trating the overlying nucellar tissue; while in *Gnetum* it enters the embryo sac and encounters the free egg nuclei (fig. 531).

Embryo. — The development of the embryo of Gnetales shows a remarkable modification of the usual gymnosperm method, and varies in accordance with the structure of the gametophyte in each genus. In all cases the embryo has two cotyledons.

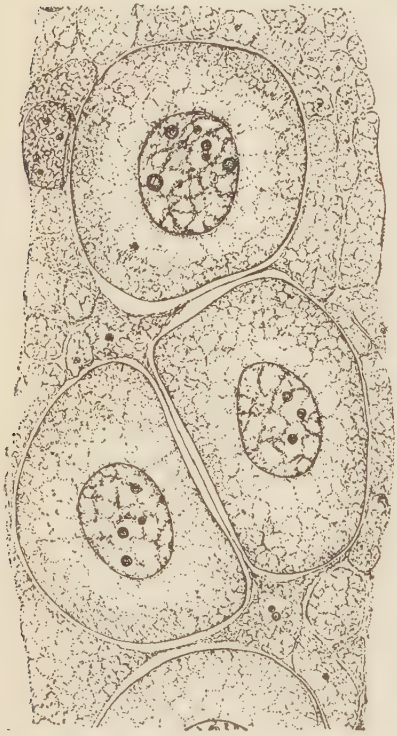


FIG. 534. — Embryo of *Ephedra:* three of the eight free proembryonal cells. — After LAND.

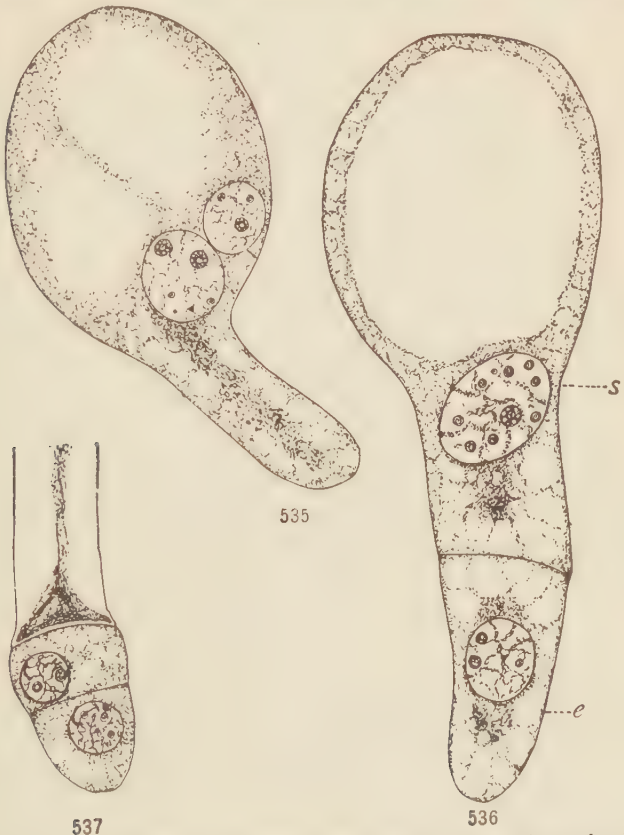
Ephedra. — In *Ephedra* there is free nuclear division within the egg until eight free nuclei appear, and then these nuclei enter into the organization of eight free cells (the proembryonal cells, fig. 534). Two or more of these independent proembryonal cells may function as follows: the nucleus divides; the cell develops a prolongation like a pollen tube (fig. 535), which penetrates the surrounding endosperm, and into its tip one of the nuclei passes. Later the tip of this tube, containing the nucleus, is cut off by a wall (fig. 536), and from this cell the embryo is developed (fig. 537).

Tumboa. — In *Tumboa* the fusion nucleus (within the prothallial tube) is used in the formation of a free and independent cell, which then behaves as do the independent proembryonal cells of *Ephedra*. It should be noted that in this case the stage of free nuclear division in embryo formation has disappeared, and the first division of the fertilized egg is accompanied by wall formation, which is an angiosperm condition.

Gnetum. — In *Gnetum* the fertilized eggs in the micropylar chamber of the embryo sac behave as in the case of *Tumboa*, and as do the proembryonal cells of *Ephedra*, the tubular prolongation penetrating the endo-

sperm tissue, which finally replaces the nucellar tissue. In both *Tumboa* and *Gnetum*, therefore, the general behavior of the angiosperm egg has been reached.

Conclusions. — It is evident that Gnetales show remarkable angiosperm tendencies, which may be summed up as follows: true vessels in



FIGS. 535-537. — Embryo of *Ephedra:* 535, one of the proembryonal cells whose nucleus has divided and which has begun to form a tubular elongation; 536, both nuclei in the tubular elongation and a wall formed between them, one cell (*s*) elongating to form the suspensor, the other (*e*) to form the embryo; 537, embryo beginning to form at the end of the suspensor. — After LAND.

the secondary wood; the final elimination of archegonia and the organization of independent eggs; and an embryogeny in which free nuclear division in the fertilized egg has disappeared. The elimination of arche-

gonia seems to be associated with the tendency to differentiate the egg nucleus earlier and earlier in the history of the gametophyte, and when this differentiation occurs before wall formation, archegonia are no longer possible. The compound strobili of Gnetales also, both staminate and ovulate, with their more or less differentiated bractlets investing the stamens and ovules, suggest the inflorescence of certain angiosperms.

There is no sure record of Gnetales as fossils, and therefore all the evidence available indicates that they are relatively modern among gymnosperms. *Ephedra* is evidently related to the Coniferales; and *Tumboa* and *Gnetum* are just as evidently related to *Ephedra;* so that it is altogether probable that the Gnetales represent a somewhat modern offshoot from the Coniferales.

B. ANGIOSPERMS

General character. —The angiosperms represent the culmination of the plant kingdom, and are plants not only of the highest rank, but also of the greatest importance to man. Probably they constitute also the greatest group of plants in the number of species, which is approximately 125,000. When this vast assemblage of species is contrasted with the 450 living gymnosperms and the 4000 living pteridophytes, it is evident that the angiosperms form by far the largest part of our vascular vegetation. It is also the most modern vascular group, being absolutely unknown in the Paleozoic, and not very abundant until late in the Mesozoic. The conspicuous superficial character of the group, as contrasted with gymnosperms, is implied in the name, the ovule being enclosed by the *carpel* (megasporophyll), so that the pollen grain does not reach the ovule, but rests on the surface of the carpel.

The great groups. —The two primary divisions of angiosperms are the *Dicotyledons* and the *Monocotyledons,* and the four prominent characters used in distinguishing them are as follows: (1) the embryo of a monocotyledon has a single terminal cotyledon and a laterally developed stem tip; while the embryo of a dicotyledon has a terminal stem tip and laterally developed cotyledons (usually two); (2) in the stem of a monocotyledon the vascular bundles are scattered; while in a dicotyledon they are arranged so as to form a vascular cylinder enclosing a pith; (3) the leaves of monocotyledons have a closed venation, that is, veinlets do not end freely in the margin, which is therefore entire; while the leaves of dicotyledons have an open venation, veinlets ending freely in the margin, which is often variously toothed or lobed; (4) the

flowers of monocotyledons have their members in sets of three; while the flowers of dicotyledons have their members in sets of five or four.

These characters are by no means of equal value, the character of the embryo being the only one without serious exception. There are monocotyledons with vascular cylinders, with open venation, and with flowers not in threes; and there are dicotyledons with scattered vascular bundles, with closed venation, and with flowers in threes. It is not so much a single character, therefore, that distinguishes a monocotyledon from a dicotyledon, as a combination of characters.

There are recognized also two great divisions of dicotyledons, the *Archichlamydeae* and the *Sympetalae*, and the conspicuous character which distinguishes them is implied in their names. The Archichlamydeae have either no petals or petals entirely separate from one another (free), and this is recognized as the primitive condition of the perianth (*chlamys*); while in the Sympetalae the petals develop so as to form tubes of various kinds. This distinction is superficial and breaks down in certain cases, but it holds generally and is convenient.

These three great groups of angiosperms are related to one another as follows: the Archichlamydeae are recognized as including the most primitive angiosperms; from the more primitive Archichlamydeae the monocotyledons probably have arisen as a special branch; while from the more advanced Archichlamydeae the Sympetalae have arisen and are clearly the highest group of angiosperms. It will be necessary to keep in mind these three groups and their relationships in order to understand the following discussion.

Stem

A description of the general structure of a vascular stem has been deferred to angiosperms, whose stem may be taken as an illustration of the general features of all vascular stems.

Elongation. — The tip of the stem is the *growing point*, consisting of a group of very actively dividing (*meristematic*) cells. Among pteridophytes this group of meristematic cells is usually represented by a single apical cell. All the tissues of the stem are derived from the cells of the growing point, whose activity very soon results in the appearance of three more or less distinct generative regions: (1) *dermatogen*, which later forms the *epidermis;* (2) *periblem*, which later forms the *cortex;* and (3) *plerome*, a central cylinder which forms the *stele*, in which the vascular elements appear (fig. 538).

Epidermis. — The dermatogen passes into the epidermis, which is usually a single layer of protective cells closely interlocked and with relatively impervious walls, but pierced by stomata. In case the stem increases in diameter, as in dicotyledonous trees, the epidermis is usually ruptured and destroyed, and another protective layer is developed by the cortex, as described below.

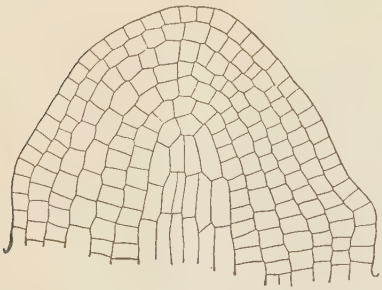


FIG. 538. — Stem tip of *Hippuris* (a dicotyledon), showing dermatogen (outermost layer), periblem (the five layers beneath the dermatogen), and the plerome (central region of more elongated cells). — After DEBARY.

Cortex. — The periblem produces the cortex (figs. 539, 541), which is a hollow cylinder of living cells. It is exceedingly variable in structure, but is characterized by containing chlorophyll tissue abutting against the epidermis; and if it is thick enough, there is also a deeper region of the cortex free from chlorophyll. The layer of cortical cells abutting against the stele often forms a very distinct bounding layer, like an inner epidermis, and is called the *endodermis* (fig. 379). In the cortex, strands of fibrous cells may be developed, and cavities or canals of various kinds may occur.

In case the stem increases in diameter, the cortex develops a meristematic layer known as the *phellogen* or *cork cambium* (fig. 539), which forms *cork cells*, a very impervious kind of cell (see p. 318). Continuous activity of the phellogen within results in an increasing thickness of the sheet of cork cells without, and such sheets form a most efficient protection. The chlorophyll tissue beneath the cork cells maintains connection with the air for a time through special structures, called *lenticels* (fig. 540), interrupting

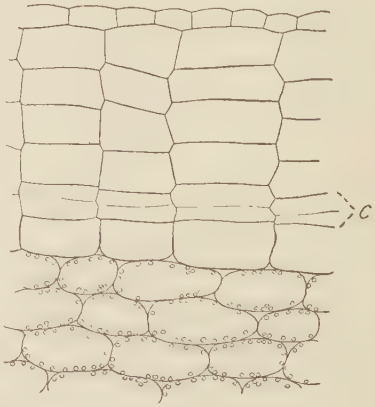


FIG. 539. — Transverse section of outer portion of cortex of a geranium, showing the cork cambium or phellogen (*c*) cutting off layers of cork cells (four such layers beneath epidermis); below are chlorophyll-containing cells of the cortex.

the cork. The phellogen layer may be developed at various depths in the cortex, and all the cortical cells outside the cork die, being cut off from the supplies within.

Stele. — The plerome cylinder behind the growing point passes below into the stele containing the vascular elements. The outermost layer of stelar cells, abutting against the endodermis, is called the *pericycle*. The first xylem elements to appear are small in caliber, and of the *spiral* kind (fig. 542), a kind especially adapted to a region of rapid elongation. These groups of spiral vessels are called the *protoxylem* (fig. 541), and the later vascular elements form the *metaxylem* (fig. 541). In case there is a cambium, a *secondary xylem* is

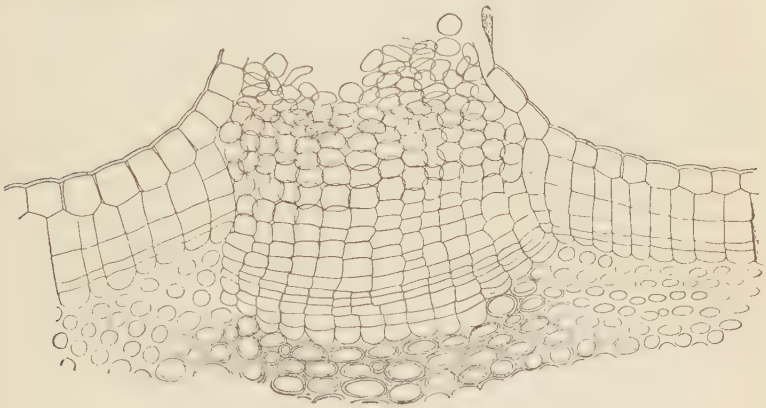


FIG. 540. — Section of the lenticel of elder. — After STRASBURGER.

formed. In neither metaxylem nor secondary xylem do vessels of the spiral kind usually occur, but vessels of larger caliber (fig. 541), notably the *pitted vessels* or *dotted ducts* so called on account of the thin spots left in a generally thickened wall (fig. 544). In gymnosperms (except Gnetales) there are no true vessels (*tracheae*), but *tracheids* (single cells tapering at each end) with thin spots in the wall, so characteristic in appearance as to be called bordered pits (fig. 547). In pteridophytes, this same kind of xylem element is represented by tracheids with transversely elongated pits, known as *scalariform* (ladder-like) vessels (fig. 548).

In forming tracheids or tracheae, the protoplasts of the living cells gradually disappear as the characteristic thickening of the wall is formed, so that the completed vessels are dead cells. Tracheids are single cells

thus formed; while tracheae (true vessels) are developed by a fusion of cells end to end, so that a continuous tube of considerable length may be formed. A system of tracheae always ends in tracheids, which are therefore at least the end cells of any vascular system.

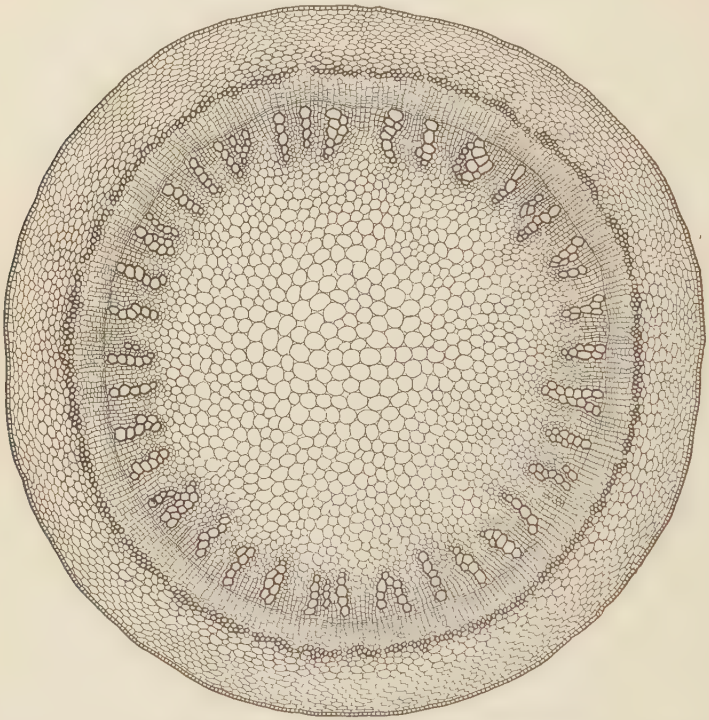


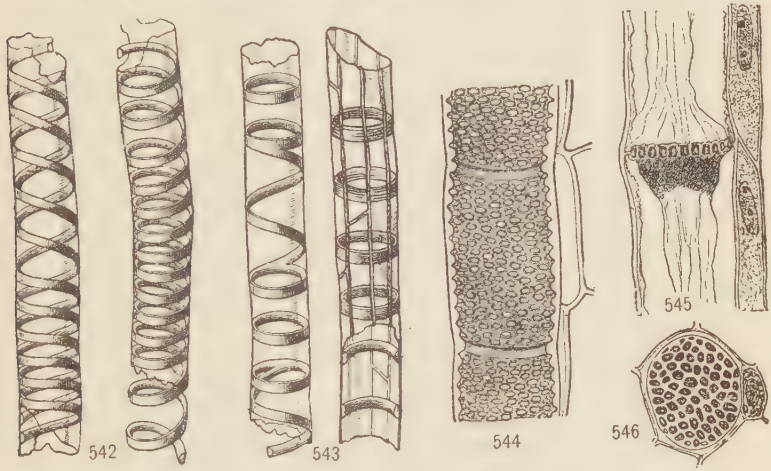
FIG. 541. — Transverse section of vascular cylinder of a young dicotyledon (*Ricinus*): the regions, beginning outside, are epidermis (single layer of cells); cortex (a zone of several layers), including an almost continuous band of fibrous cells (heavy walls); a zone of several layers (the outer ones being phloem, the inner cambium); the zone of xylem strands (separated by pith rays, the innermost vessels in each strand being protoxylem, the outer and larger ones metaxylem); and the pith.

The characteristic element of the phloem is the *sieve vessel* (fig. 545), so named because in the wall there occur definite areas full of perforations known as *sieve plates* (fig. 546). These vessels also arise by cell fusion, as do the tracheae.

The vascular system. — The vascular system of dicotyledons and of monocotyledons is so different that the two groups must be considered separately.

Dicotyledons. — The vascular system of dicotyledons is by no means uniform, nor should it be expected in so large a group, but its general features can be indicated.

In the mature stem the vascular system consists of a hollow cylinder composed of vascular bundles and inclosing the pith (a siphonostele) (figs 541, 549). Traversing the vascular cylinder from the pith to the cortex, and hence separating the bundles, are the pith rays. The bundles are collateral endarch, and also *open;* that is, there is a *cambium* between the xylem and phloem strands which forms secondary xylem

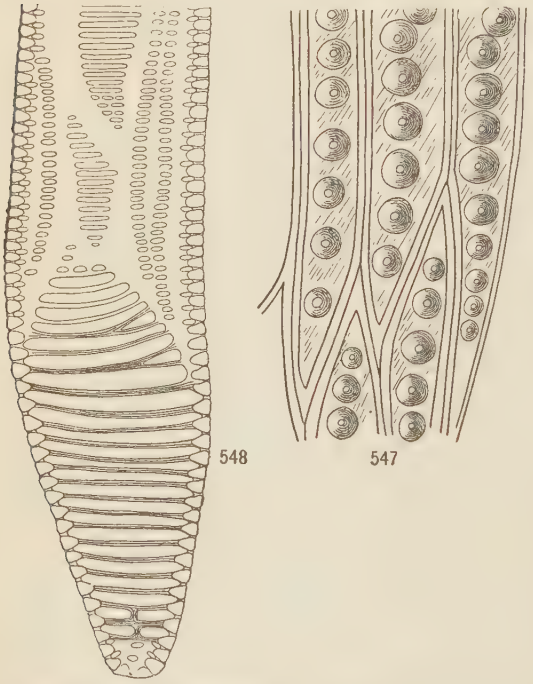


FIGS. 542–546. — Vascular elements of an angiosperm: 542, spiral vessels (of protoxylem); 543, spiral and annular vessels; 544, dotted duct (characteristic of metaxylem and secondary xylem); 545, sieve vessel (of phloem) with companion cell; 546, sieve plate, with section of companion cell. — 542, 543, after BONNIER and SABLON; 544, after DEBARY; 545, 546, after STRASBURGER.

and phloem. The secondary wood (xylem) differs from that of the gymnosperms in containing true vessels (*tracheae*) instead of tracheids, and most characteristic among these vessels are the dotted ducts (fig. 544). The phloem also differs from that of the gymnosperms in that the sieve vessels have *companion cells* (figs. 545, 546). No trace of mesarch structure is seen, even in the cotyledons, which seems to indicate that the angiosperms are further removed from the ferns than are the gymnosperms.

The only primitive suggestion that remains in the vascular system of the stem is the presence of leaf gaps in the vascular cylinder, connected

with the insertion of the leaf traces. It will be remembered that the presence of leaf gaps is a feature of the ferns, in contrast with the other groups of pteridophytes; and their appearance in the dicotyledons is taken to be one indication that this group is connected with ferns, either through gymnosperms or directly. In tracing the development of the vascular system in a seedling dicotyledon, it is interesting to note that the stem cylinder often begins as a protostele, and more or less rapidly becomes a siphonostele.



FIGS. 547, 548. — Tracheids: 547, those of gymnosperms, with bordered pits (after CHAMBERLAIN); 548, the scalariform tracheids of ferns (after DEBARY).

Monocotyledons. — The monocotyledons were once thought to be the primitive angiosperms, but the study of their vascular anatomy has been chiefly instrumental in suggesting the probability that they are derived from dicotyledons. The evidence is obtained from a study of the development of the vascular system from the earliest stages of the seedling to the adult stem. A transverse section of an adult stem usually shows "scattered" vascular bundles (fig. 550), quite unlike the arrangement into a hollow vascular cylinder characteristic of the dicotyledons. In studying the development of this stem, however, four stages are often recognized. In the earliest stage the cylinder may be a protostele; and this passes more or less quickly into the second stage, that of the siphonostele, in which the cylinder is just that of a dicotyledon, with its collateral bundles. This means that an embryonic stage of a monocotyledon is the permanent, adult condition of a dicoty-

ledon. In some monocotyledons this stage persists, and in these cases the adult stems resemble those of dicotyledons.

In the third stage of development the collateral bundles gradually become transformed into *amphivasal* bundles; that is, bundles in which the xylem surrounds the phloem (fig. 551). This transformation is very evident, the xylem of the collateral bundle gradually extending about the phloem until finally it surrounds it completely. All the intermediate stages in this extension of the xylem about the phloem may be found. The amphivasal bundle is characteristic of the mature stems of monocotyledons. In the seedlings, the leaves, and floral axes, the bundles are collateral (the dicotyledon type);

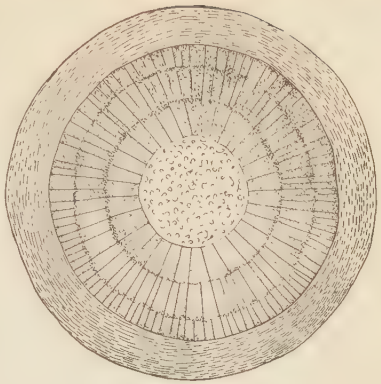


FIG. 549. — Transverse section of stem of dicotyledon (box elder), showing vascular cylinder composed of three growth (annual) rings of xylem formed by the cambium.

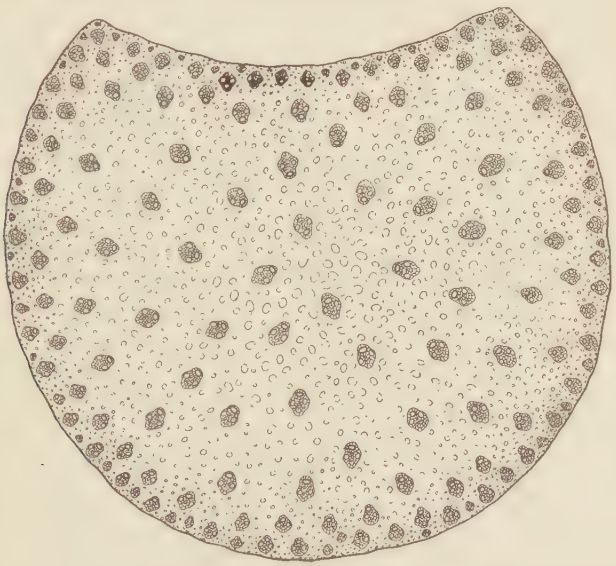


FIG. 550. — Transverse section of stem of monocotyledon (corn), showing the "scattered" vascular bundles.

so that it seems evident that the amphivasal (monocotyledon) type of bundle is more recent than the collateral (dicotyledon) type.

While the transformation of collateral to amphivasal bundles is progressing, the bundles of the cylinder become more and more dissociated; some bundles enter the pith region, the definite outline of a hollow cylinder is broken up, and a transverse section of the stem shows

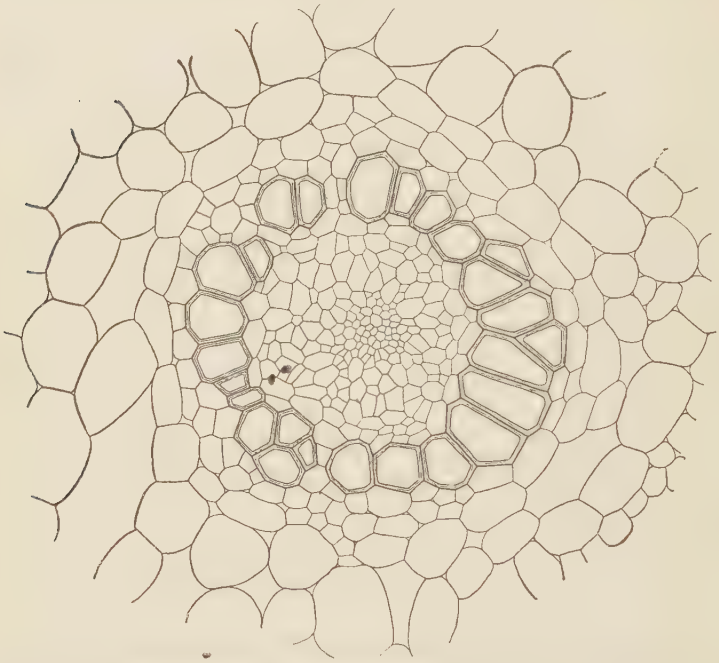


FIG. 551. — Transverse section of amphivasal bundle of *Acorus* (a monocotyledon), showing the xylem completely surrounding the phloem.

vascular bundles scattered through the stele (fig. 550). This development of pith (medullary) bundles and the disorganization of the cylinder is the fourth stage.

Of course there are monocotyledons which do not pass through all these stages, stopping at the second (when they are like dicotyledons), or at the third (when the cylinder is retained but the bundles are amphivasal). There are also dicotyledons in which medullary bundles develop and the cylinder is broken up (as in *Castalia*, *Podophyllum*, certain species of *Ranunculus*, etc.), and even some in which amphivasal

bundles are formed (as in *Rheum*). It is interesting to note that these dicotyledons with broken-up cylinders belong in the region of the Archichlamydeae from which the monocotyledons are believed to have arisen.

Root

The structure of roots is relatively uniform throughout vascular plants, so that a general description may apply to all groups.

Elongation. — The growing point of the root is not at the surface of its tip, but just beneath, being covered by a tissue of protective cells called the *root cap* (fig. 552). As a consequence, the group of meristematic cells within the root tip forms four generative regions: (1) dermatogen, (2) periblem, and (3) plerome, as in the stem; to these is added (4) *alyptrogen* which forms the root cap, the latter renewed from beneath as it wears off outside (fig. 552).

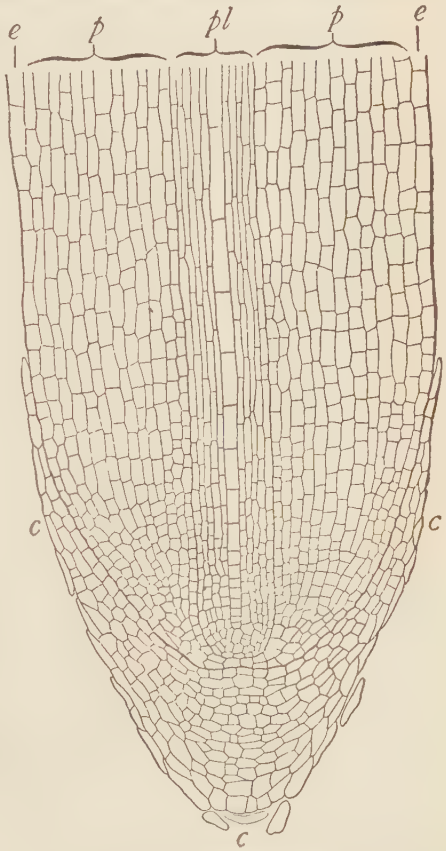


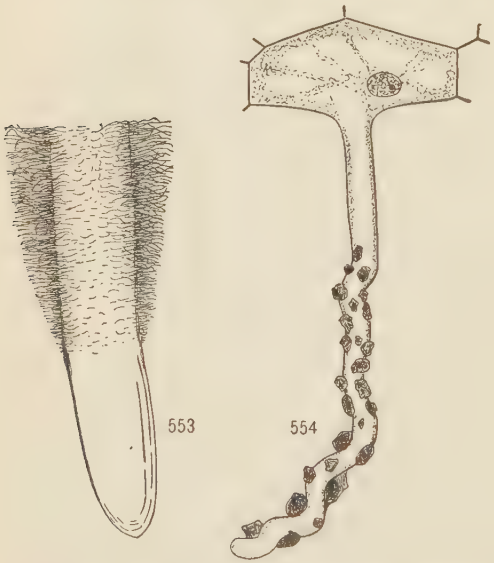
FIG. 552. — Longitudinal section of root tip of spiderwort (*Tradescantia*), showing root cap (*c*), dermatogen (*e*), periblem (*p*), and plerome (*pl*). — After COULTER.

Root hairs. — Behind the root cap the *root hairs* appear, which are produced by the epidermal cells, and are really enormous extensions of the surface of epidermal cells (figs. 553, 554). Root hairs are relatively short lived, but new ones are formed constantly as the root elongates.

The vascular system. — The vascular anatomy of the root is of the same general type throughout vascular plants. The vascular cylinder

is of the most primitive type, being solid (with xylem at the center) and exarch. However, it is not concentric, the xylem developing towards the center from two or more protoxylem points near the periphery of the stele, and between these radiating strands of xylem separate phloem strands occur (fig. 555). This arrangement of phloem and xylem, in which they occur on alternating radii, is called the *radial* arrangement.

In the secondary thickening of roots (figs. 556, 557), a cambium is developed, which forms secondary xylem inside the phloem; the two,



FIGS. 553, 554. — Root hairs: 553, of corn, showing relation to root tip; 554, of wheat, showing relation to an epidermal cell and the close contact with soil particles.

FIG. 558. — Endogenous origin of root branches: longitudinal section of root of arrow leaf, showing the branches starting from the vascular cylinder and penetrating the cortex. — After COULTER.

therefore, hold the same relation to one another as do the xylem and phloem of a collateral bundle. Continued activity of this cambium results in a cylinder of collateral bundles, made up of phloem and secondary xylem; and the radiating arms of the primary xylem are at the bottom of the primary pith rays. Of course, the cambium also forms secondary phloem within the older phloem. By this secondary growth the vascular cylinder of a root may soon lose any appearance of its primitive radiate structure, and assume the appearance of a dicotyledonous stem, with collateral bundles.

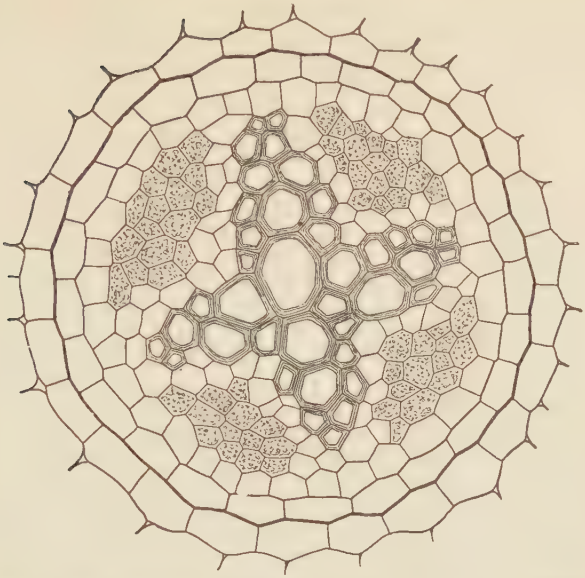
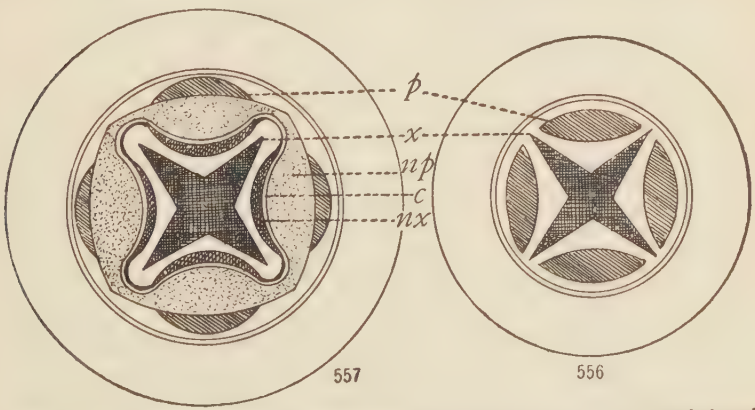


FIG. 555. — Partly diagrammatic transverse section of vascular cylinder of root of *Ranunculus:* the two outermost layers belong to the cortex, the inner one being the endodermis; the next layer (outermost one of the stele) is the pericycle; in the center is the group of xylem vessels, extending in four rays to the pericycle; the outermost xylem vessels of each ray are protoxylem, the metaxylem having developed towards the center in four converging lines; between the xylem rays are the four groups of phloem (shaded).



FIGS. 556, 557. — Diagrams to show secondary thickening in root, 556 being the primary condition, 557 the secondary; *x*, primary xylem; *p*, primary phloem; *c*, cambium; *nx*, secondary xylem; *np*, secondary phloem. — After COULTER.

The branches of a root are formed at the periphery of the vascular cylinder and push through the cortex, this *endogenous* origin being in sharp contrast with the method of origin of stem branches (fig. 558).

Leaf

The structure of an angiosperm leaf is in every essential the same as that of a pteridophyte leaf, and should be clear at this point. For those

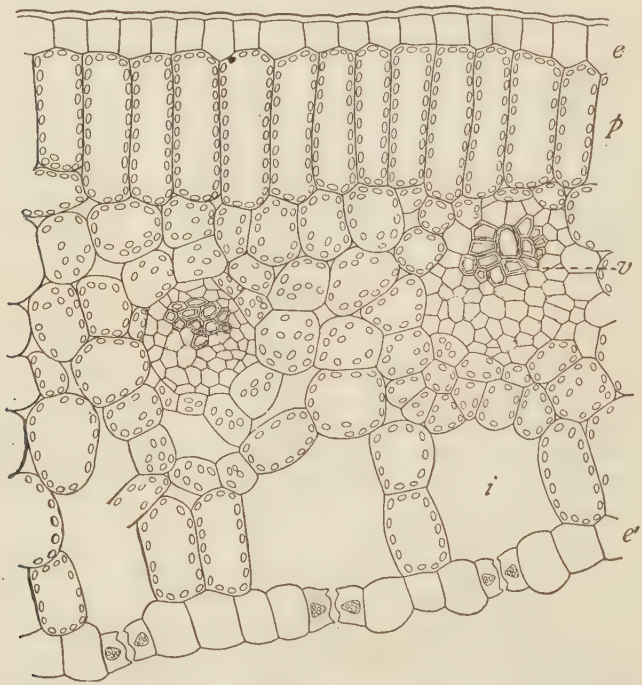
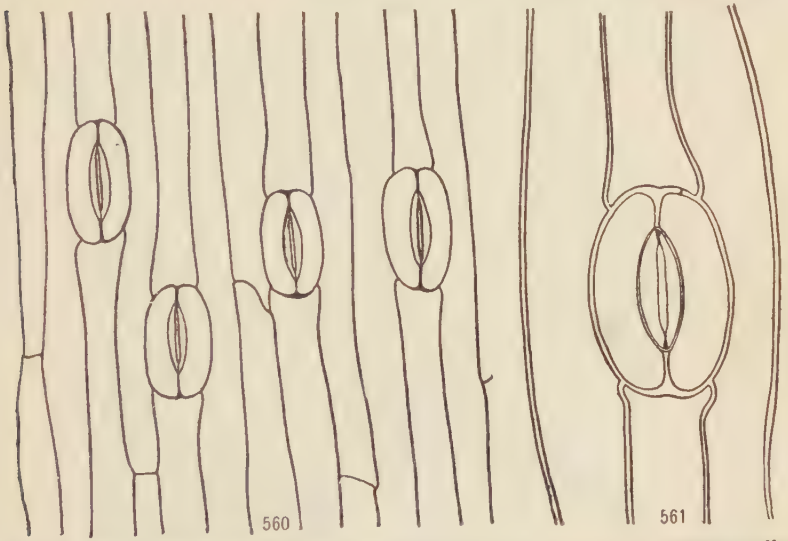


Fig. 559. — Transverse section of lily leaf: beginning above, the regions are the upper epidermis (*e*); the palisade layer (*p*); the region of spongy tissue (extending to the lower epidermis), with intercellular spaces and vascular strands (*v*), the cells containing chlorophyll; and the lower epidermis (*e'*), in which sections of three stomata are seen, each opening into a large intercellular chamber (*i*). — After Coulter.

unfamiliar with this structure, it may be pointed out that the essential features of an ordinary dorsiventral leaf are as follows: a layer of close-fitting or even interlocked epidermal cells above and below, in which stomata are developed (figs. 559–561); between the epidermal layers the *mesophyll* region, whose cells contain chloroplasts (fig. 559);

often two regions of mesophyll (the *palisade region* of vertically elongated and close-lying cells, and the *spongy region* of rounded and loosely packed cells, leaving a labyrinth of intercellular spaces); and the *veins*, of varying order (fig. 559, *v*), which traverse the mesophyll and contain the vascular strands (conducting system) connecting with



FIGS. 560, 561. — 560, surface view of epidermis of leaf of lily, showing epidermal cells and stomata; 561, a single stoma more highly magnified. — After COULTER.

those of the stem and root, and also strands of mechanical or supporting tissue. Such a structure provides protection (epidermal layers) for the mesophyll cells, an internal atmosphere bathing the mesophyll cells and communicating with the external atmosphere through the stomata, a conducting system, and a mechanical framework.

FLOWER

General character. — The flower is a very characteristic structure of angiosperms, but it is impossible to define it with exactness, so as to apply to all angiosperms and to no other group. In passing from gymnosperms to angiosperms there is a gradual transition from the structure called a strobilus to that called a flower or an inflorescence. The most characteristic feature of the flower of angiosperms is the presence of a perianth associated with the sporophylls. In its full expres-

sion, the perianth consists of two sets of members, *sepals* and *petals*, which in general are foliar in nature, but differ more or less distinctly from the ordinary bracts or leaves of the plant (fig. 562). They seem to have been derived, historically, from adjacent sporophylls and adjacent bracts or foliage leaves ; in any event, they are intercalated as distinct members between the bracts or foliage leaves on the one side, and the sporophylls on the other. It is not clear what was the most primitive condition of the flower among angiosperms; whether it began with

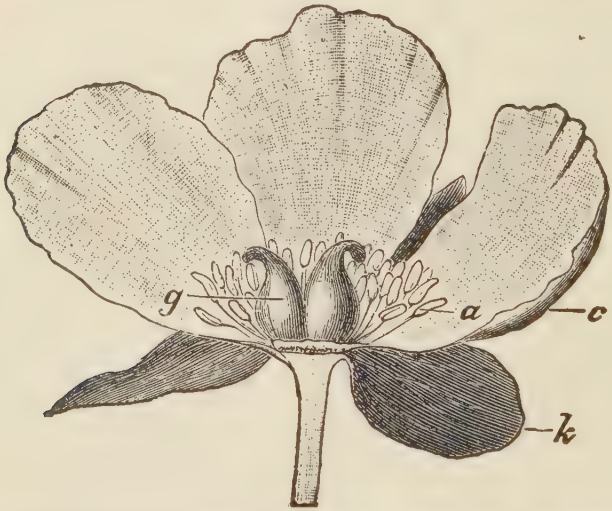
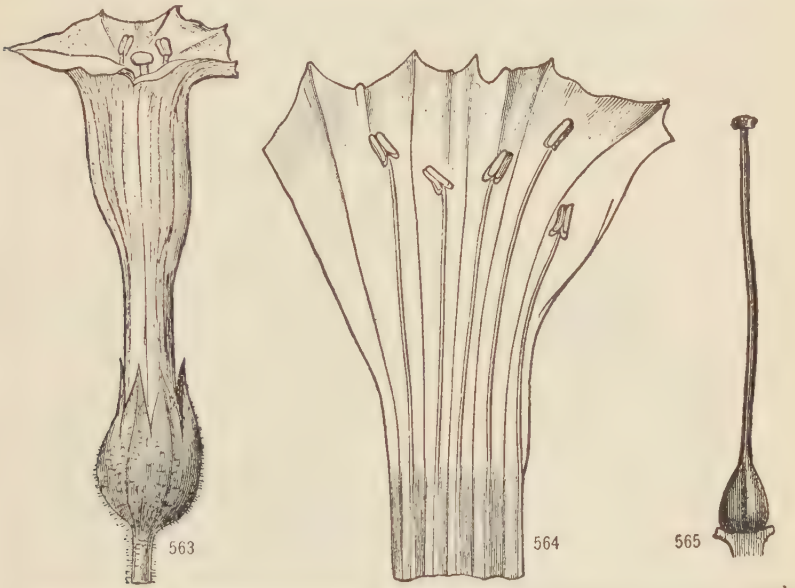


FIG. 562. — Section of flower of peony, showing sepals (*k*), petals (*c*), numerous stamens (*a*), and apocarpous carpels (*g*). — After STRASBURGER.

a fully developed perianth, which in certain groups became reduced or even suppressed ; or whether it began with no perianth, which first appeared in very simple form and gradually became more highly developed and complex. Both views have support. In any event, there are certain general facts and tendencies of the flower which are evident.

Differentiation of perianth. — A series of flowers can be arranged with those having no perianth (*naked*) at one end, and those with a sharply differentiated *calyx* (sepals) and *corolla* (petals) at the other. Between these two extremes there will be found flowers with inconspicuous bracts, those with bracts more distinctly perianth-like in arrangement, those with a perianth differing in texture from bracts but not differentiated into two sets. It is evident that this series may have developed

in either direction; that is, either by the gradual reduction and final elimination of the perianth (a reduction series), or by the gradual appearance and differentiation of the perianth (an ascending series). In the one case the naked flowers, for example, would be reduced flowers; in the other case they would be primitive flowers. There is every reason to believe that evolution has taken place in both these directions, and



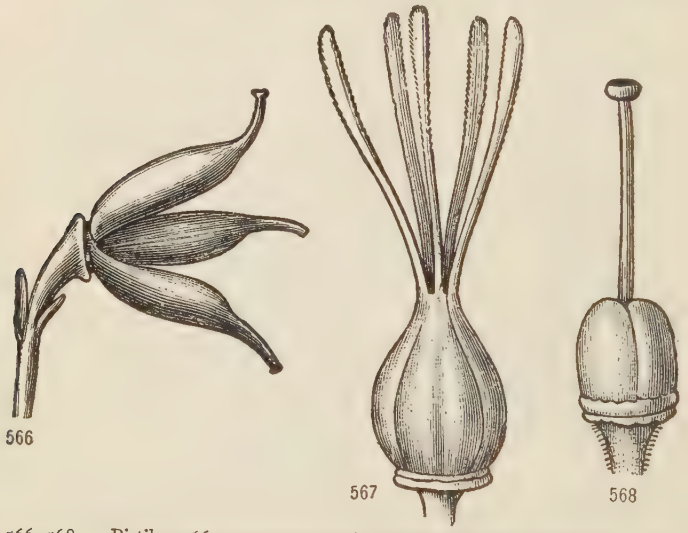
FIGS. 563–565. — 563, sympetalous flower of tobacco (*Nicotiana*); 564, an opened corolla tube, showing the stamens apparently attached to it; 565, the syncarpous pistil. — After STRASBURGER.

that what are known as simple flowers are sometimes primitive and sometimes reduced.

Spiral to cyclic. — A very evident tendency in the evolution of the angiosperm flower is to pass from what is called the spiral condition to the cyclic condition. In a strobilus the bracts and sporophylls are spirally arranged upon a more or less elongated axis, and are indefinite in number; and this same condition occurs in the flowers of certain angiosperms. Beginning with this strobilus-like flower there is a tendency to shorten the floral axis (*receptacle*), which results in a closer spiral of flower parts, and finally reaches the cyclic stage, in which there is a cycle for each kind of organ. At the same time, the receptacle

broadens, so that the final stage is one in which the succession of cycles seems to be centripetal rather than acropetal.

Associated with the appearance of the cyclic stage is the establishment of a definite number of organs for each cycle. For example, the definite floral number for cyclic monocotyledons is three, but there are many spiral monocotyledons with no definite number; the definite floral number for cyclic dicotyledons is usually five or four, but there is a host of spiral dicotyledons in which the numbers are indefinite. The cyclic condition is not necessarily attained simultaneously by all the regions of



FIGS. 566–568. — Pistils: 566, apocarpous; 567, syncarpous with free styles; 568, completely syncarpous. — After BERG and SCHMIDT.

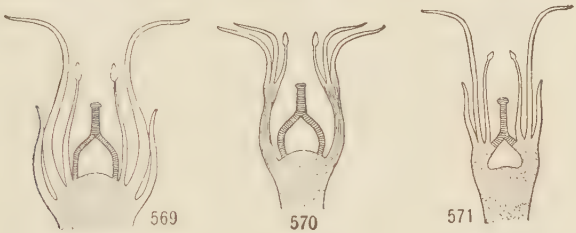
the flower. For example, in the buttercup the sepals and petals usually show the definite cyclic number five, but the stamens and carpels are still in the spiral condition of indefinite numbers (fig. 562).

Zonal development. — Another evident tendency among the flowers of angiosperms is the so-called coalescence of members of the same set. For example, the zone of tissue upon a receptacle which is giving rise at several points to a cycle of separate petals, sooner or later begins to develop uniformly, resulting in a corolla tube instead of several petals (fig. 563). This is called *zonal development*, and the sooner it begins the more completely tubular does the corolla become. This tendency to zonal development is observed in all the floral cycles, and this condition

is poorly expressed in the terms *synsepalous*, *sympetalous*, *monadelphous*, and *syncarpous*. The syncarpous condition (*syncarpy*) is extremely common (fig. 568); but the sympetalous condition (*sympetaly*) is noteworthy as giving name to one of the three divisions of angiosperms.

All such terms as "united," "fused," "coalescent," and their technical equivalents suggest a very wrong impression as to the origin of the structure concerned. The separate parts implied in the words "united," etc., never had a separate existence. For example, in many cases separate petals occur; and where there is zonal development they are not separate, but this does not mean that they have "united" or "coalesced."

Hypogyny to epigyny. — Zonal development often involves more than a single set. In sympetaly the stamen zone is also usually involved, so



FIGS. 569–571. — Diagrams to show structure of hypogynous (569), perigynous (570), and epigynous (571) flowers. — After GANONG.

that the stamens seem to arise from the tube of the corolla (fig. 564). There are three conditions in reference to zonal development that includes more than one set which are important to note, for they have to do with a distinct evolutionary tendency of the flowers. The most primitive condition is one in which the sets are entirely free from one another (unless it be the corolla and stamens), in which case the flower is *hypogynous*, meaning that the three outer sets arise from beneath the carpel set (fig. 569). In another condition, zonal development involves the three outer sets, resulting in an urnlike structure surrounding the carpels, from the rim of which the distinct sepals, petals, and stamens arise. In this case the flower is *perigynous*, meaning that the three outer sets seem to arise around the carpel set (fig. 570). In the last condition the zonal development involves all of the sets, leaving a cavity in the center, so that all of the sets seem to arise from the top of the ovary. In this case the flower is *epigynous*, meaning that the floral members seem to stand upon the ovary (fig. 571). Epigyny is regarded

as an advanced character, and is one of the prominent features of the families considered as highest.

Irregularity. — There is also often a tendency for one or more of the sets to become *irregular* (zygomorphic), a tendency noteworthy chiefly among petals. This means that the corolla is not composed of similar petals, as is true of *regular* (actinomorphic) flowers, but that the petals differ decidedly in form, as, for example, in a sweet pea. This tendency to irregularity is not a general one, but is characteristic of certain groups.

These various tendencies are found in the different groups in all stages of development, so that the relative rank of a group is determined by the combination of its stages. For example, a naked, spiral, hypogynous flower, in which there is no zonal development, would have the most primitive combination; while a cyclic, sympetalous, syncarpous, and epigynous flower would have the most advanced combination.

Organogeny. — The *organogeny* of a flower has to do with the development of the floral members, the most noteworthy fact being the order of succession of the different sets. In a spiral flower the order of succession is necessarily *acropetal;* that is, the sets arise successively towards the apex of the receptacle. This succession, therefore, is sepals, petals, stamens, carpels. If this succession is maintained in a cyclic flower, the acropetal succession, of course, appears centripetal. But with the shortening and broadening of the floral axis (receptacle), the primitive succession is often broken up. For example, in Compositae (the highest family) the succession is petals, stamens, carpels, sepals, which is a striking shift in the position of the sepals; while in *Capsella* (shepherd's purse) the succession is sepals, stamens, carpels, petals.

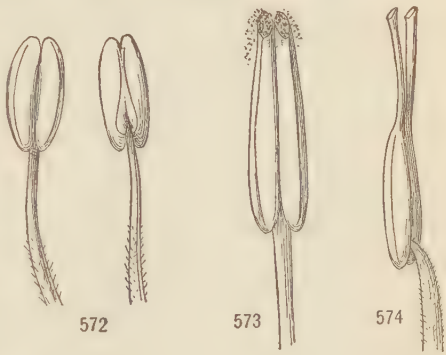
Relation of sporangia. — The flowers of angiosperms are prevailingly bisporangiate; that is, stamens and carpels occur in the same flower (fig. 562). In the case of monosporangiate flowers two conditions are possible: the staminate and carpellate flowers may occur upon the same plant (*monoecious*) or upon different plants (*dioecious*).

Stamen

General character. — The stamen is the organ bearing microsporangia, and therefore is the equivalent of the microsporophyll of gymnosperms. The sporangia are usually four in number, but they vary from one to many. Usually the stamen is differentiated into two distinct regions: the *anther*, which is the region bearing the sporangia; and the *filament*.

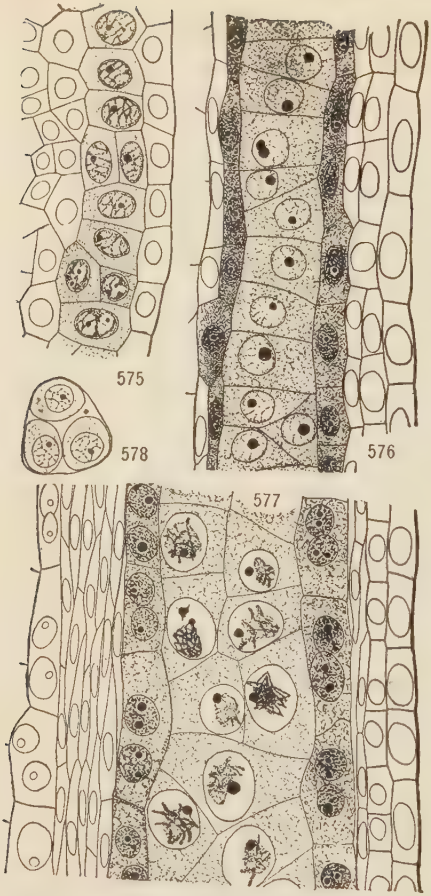
which is the more or less elongated, stalklike region (figs. 572–574). It should be noted that such a term as anther is one of convenience rather than of morphological exactness, for it is made up of a complex of sporangia and sporophyll.

Microsporangia. — The sporangia develop as in gymnosperms, being of the eusporangiate type. A transverse section of a very young anther shows a mass of homogeneous tissue invested by the epidermis. The layer just beneath the epidermis (hypodermal layer) is potentially sporogenous; but usually it becomes actually sporogenous in four regions, which in transverse section show a variable number of cells (one to several). Of course these regions of initial cells are really four longitudinal, hypodermal bands of varying width. Each one of these bands of initials divides periclinally, forming two layers of cells (fig. 575). The outer layer (just beneath the epidermis) is the primary wall layer; the inner one is the primary sporogenous layer. The primary wall layer divides further, forming several (usually three to five) wall layers (fig. 576). The outermost wall layer is usually much modified, the cells becoming large and conspicuously banded, forming the so-called *endothecium* (fig. 580), a layer that assists in the dehiscence of the sporangium. The innermost wall layer usually becomes transformed into a portion of the *tapetum*, the nutritive layer of the sporogenous tissue (figs. 576, 577). The intermediate layers are the *middle layers*, and usually become more or less flattened and disorganized through the activity of the tapetum. A section through a completed sporangium wall, therefore, reveals the epidermis, the endothecium, one or more middle layers, and the tapetum (fig. 577).



FIGS. 572–574. — Stamens of angiosperms, showing anther and filament: 572, ordinary type, with longitudinal dehiscence; 573, *Solanum*, with dehiscence by terminal slit or pore; 574, *Vaccinium*, with tubular prolongations of pollen sacs for dehiscence. — After KERNER.

The cells of the primary sporogenous layer usually divide two or three times (sometimes oftener, and sometimes not at all), forming the spore mother cells (fig. 577). In the two successive divisions of the mother



FIGS. 575–578. — Development of the microsporangium of *Silphium:* 575, transverse section of a small portion of a very young anther, showing the hypodermal initial cells (shaded and with large nuclei), which are beginning the periclinal division into primary wall cells (outer) and primary sporogenous cells; 576, later stage, the primary wall cells having formed three layers, the innermost (shaded) being the tapetum (nutritive layer), which is continuous about the sporogenous cells; 577, later stage, showing endothecium (layer beneath epidermis) forming, middle layer of flattened cells, tapetum conspicuous and its cells binucleate, and sporogenous tissue (after one division of primary sporogenous cells) in the mother cell stage; 578, a mother cell containing a tetrad. — After MERRELL.

cells to form the tetrads of spores (fig. 578), the reduction of chromosomes occurs. Usually the tetrads within the mother cells are of the tetrahedral type, but in some cases the arrangement is different, the four spores being in a linear series. The mature microspores (pollen grains) usually round off and separate, forming a powdery mass (fig. 580). The spore walls are two-layered, the outer layer (*exine*) being thicker and more brittle and often variously sculptured, the inner layer (*intine*) being delicate and very elastic. In the exine there are always one or more thin spots where the pollen tubes emerge, most monocotyledons having one such spot, and dicotyledons having two to many. In the pollen grains of *Ranunculus* (buttercup), for example, fifteen to thirty thin spots may be observed.

In some groups of angiosperms the spores of a tetrad do not separate, a condition once described as a compound grain. In certain cases still larger groups of spores cling together, and this tendency reaches its extreme expression in such plants as orchids and milkweeds, where all the

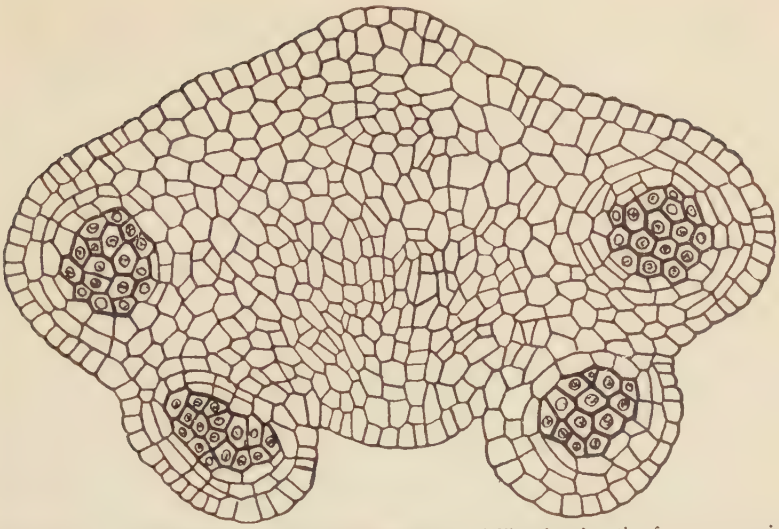


FIG. 579. — Transverse section of a young anther of lily, showing the four sporangia well advanced. — After COULTER.

spores of a sporangium cling together in one mass, called the *pollinium*.

As the four sporangia of an anther increase in size (fig. 579), the sterile tissue separating the two sporangia on each side of the anther breaks

FIG. 580. — Transverse section of a mature anther of lily, showing the sporangial cavities fused to form two pollen sacs (which are full of pollen grains); the endothecium conspicuous (just beneath a more or less fragmentary epidermis), and also the remarkable cells formed by the epidermis at the line of dehiscence (*s*); the tapetum has broken down (dotted line), and several middle layers are evident. — After COULTER.

down, and each pair becomes one continuous spore chamber or sac, called the *pollen sac* (fig. 580). The pollen sac of angiosperms, therefore, is usually composed of two coalesced sporangia. The dehiscence of the pollen sacs, in the discharge of the spores (pollen grains), is most commonly by a longitudinal slit, developed where the two coalesced sporangia join (figs. 572, 580); but sometimes they open by terminal slits or pores (fig. 573), or by openings in tubular prolongations of the pollen sacs (fig. 574), or sometimes by hinged valves.

Carpel

General character. — The carpel is a megasporophyll, and though often it does not produce the megasporangium (ovule), it always incloses it. Ovules, on account of their relation to its tip, frequently arise from the axis; so that ovules among angiosperms are both cauline and foliar in origin. The carpel is usually organized into two distinct regions: the *ovary*, in which the ovules occur; and the *style*, usually a more or less elongated and stalklike region arising from the top of the ovary (figs. 566–568). Upon the style, usually at its tip, sometimes along one side, there is exposed a special tissue that receives the pollen, known as the *stigma*. This stigma is the exposed part of a tissue which extends through the style (sometimes lining a stylar canal) and along the wall of the ovarian cavity, and forms the nutritive path of the pollen tubes on their way from the stigma to the ovules. This tissue in the style has been called *conducting tissue*, and in the ovarian cavity the *placenta*.

In cases of syncarpy, two or more carpels are organized together, forming a single ovary (fig. 567), and often a single style (fig. 568). In such cases the ovary may contain as many chambers as there are carpels, or there may be only one chamber. Since carpels may be organized singly or collectively, it is convenient to have a general term that can be applied to either kind of carpel organization, and that term is *pistil*. A *simple* pistil is one composed of a single carpel (fig. 566); while a *compound* pistil is composed of more than one carpel (fig. 567), and may contain as many chambers as there are carpels in the organization, or it may contain a single chamber.

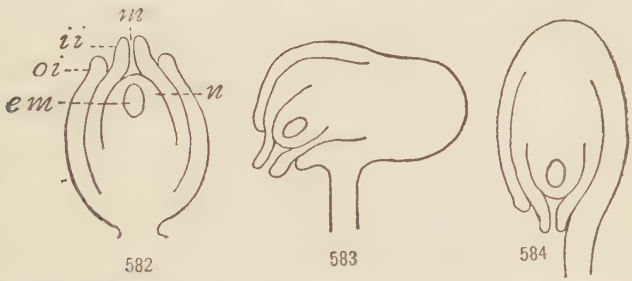
Ovule. — The ovule may arise from any free surface within the cavity of the ovary; and since this free surface involves both the carpels and the tip of the axis (sometimes prolonged into the cavity of the ovary),

the ovules may be foliar or cauline. In the different groups of angiosperms, however, the ovules are borne in very definite ways.

General structure. — In the development of the ovule, the nucellus first appears as a protrusion from the surface which bears it; later a ring arises around its base, which develops into an integument; and still

FIG. 581. — Development of an anatropous ovule, the series beginning at the left; the two integuments appear successively and gradually overtop the nucellus as the ovule becomes curved; last figure a section showing relation of the two integuments and the nucellus at maturity of ovule. — After GRAY.

later a second ring may arise outside of the first, which develops into a second integument (fig. 581). Soon the integument (or integuments) overtops the nucellus, and where it closes in over the nucellus there is left a narrow, more or less elongated passageway, the *micropyle* (fig. 582). Among the Archichlamydeae and monocotyledons there are

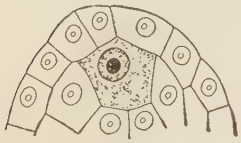


FIGS. 582–584. — Directions of ovules; 582, orthotropous; 583, campylotropous; 584, anatropous; also showing outer (*oi*) and inner (*ii*) integuments, micropyle (*m*), nucellus (*n*), and embryo sac (*em*). — After COULTER.

usually two integuments; while among the Sympetalae there is almost invariably a single massive integument.

Direction. — Important differences are shown in the directions assumed by mature ovules. Some grow straight outward from their place of origin, the axis being straight and the micropyle directed away from the point of origin; such ovules are called *orthotropous* (fig. 582), and this condition is regarded as the most primitive. In other ovules the axis

becomes curved, the micropyle being directed thus towards the surface of origin; such ovules are called *campylotropous* (fig. 583), and they are much less common than the other kinds. Far the most common kind of ovule among angiosperms is one which develops a stalk (*funiculus*) that becomes curved at the apex, so that the body of the ovule lies against it, and although the axis of the body is straight, the micropyle is directed towards the surface of origin; such ovules are called *anatropous* (inverted), the funiculus appearing as a ridge along one side of the body of the ovule (figs. 581, 584). The advantage of the anatropous ovule may be recognized when it is remembered that the pollen tube is advancing along the wall of the ovary, and the micropyles are thus brought near the wall.



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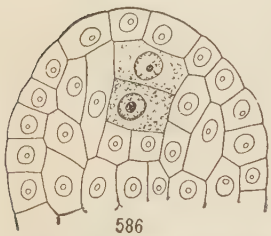

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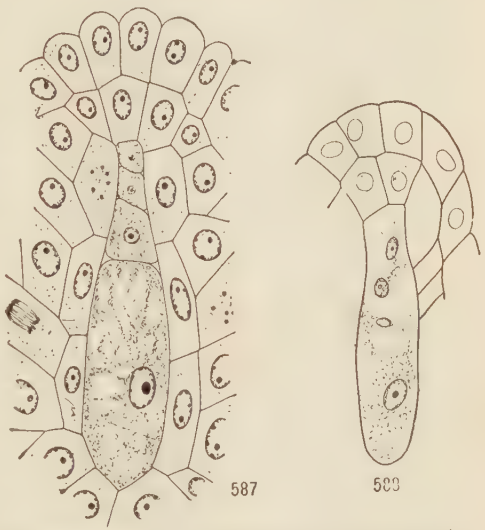
FIGS. 585, 586. — Development of megasporangium of *Salix:* 585, single hypodermal initial; 586, division of initial into primary wall cell (outer shaded one) and primary sporogenous cell. — After CHAMBERLAIN.

Development. — The megasporangium (really the nucellus) is eusporangiate in its development, resembling the microsporangium at every stage. There is usually a single hypodermal initial cell, which is soon recognized among the other hypodermal cells by its larger size and the different appearance of its contents (fig. 585). Sometimes there are two or more of these initial cells, as is the usual case in microsporangia. The large hypodermal initial divides by a periclinal wall into two cells, the outer cell being the primary wall cell, the inner one being the primary sporogenous cell (fig. 586). The wall cell may not divide (fig. 587), or there may be one or more divisions (fig. 588), or in some cases there may be several wall layers developed, as in microsporangia. The primary sporogenous cell does not divide and form more sporogenous cells, and therefore it is the megaspore mother cell. This means that when it divides, a tetrad is formed by two successive divisions, which are the reduction divisions. The tetrad of megaspores is almost always a linear row (fig. 587), which is an exceptional arrangement among microspores. It is very seldom that more than one of the megaspores matures, and that one is almost invariably the innermost one of the row, that is, the one farthest from

the micropyle. In its growth the developing megaspore encroaches upon and destroys the other megaspores and more or less adjacent tissue of the nucellus, becoming a very large cell (fig. 587), which is later the embryo sac.

This account of the development of the megasporangium includes all the events that ever occur, but in certain groups of angiosperms one or more of these events are omitted. Among the Sympetalae, for example, the hypodermal initial cell never divides into a primary wall cell and a primary sporogenous cell, but is itself the primary sporogenous cell or mother cell. This means that in this great group the wall tissue of the megasporangium has been eliminated. The same condition is found here and there in the other groups.



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FIGS. 587, 588. — Development of megasporangium: 587, tetrad of *Canna* (after WIEGAND), in which the innermost megaspore has very much enlarged; single undivided wall cell; 588, tetrad of *Eichhornia* (after WILSON SMITH), in which no walls have appeared, but three of the megaspore nuclei are degenerating; primary parietal cell divided once.

In some cases the nucleus of the mother cell divides, forming four nuclei, but walls do not separate them. Sometimes when this happens (as in *Eichhornia*) three of the nuclei degenerate and the fourth one functions (fig. 588).

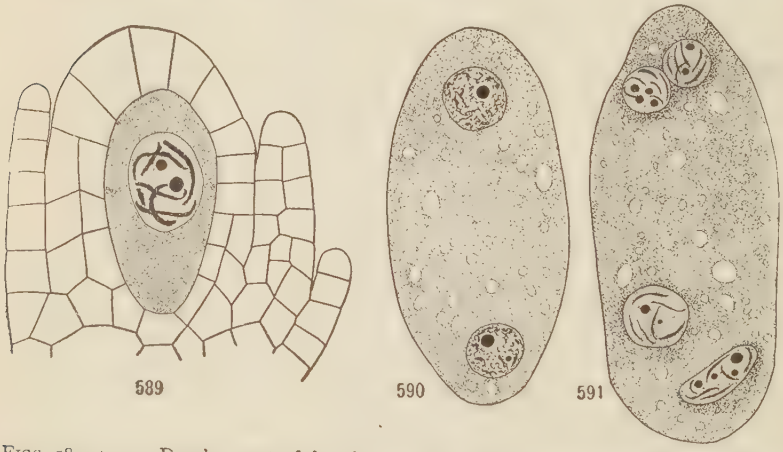
In other cases the mother cell divides only once, and one of the daughter cells functions as an ordinary megaspore in producing a female gametophyte (as in *Cypripedium*). The cell thus functioning is not really a megaspore, but two megaspores, which together form the gametophyte.

In *Lilium* and certain other forms a remarkable shortening of the history occurs. The hypodermal initial cell does not produce a wall cell, and therefore is the primary sporogenous cell or mother cell. This mother cell does not divide and form a tetrad of megaspores of the usual

kind, but the megaspores are represented by four nuclei. The mother cell, therefore, seems to behave like a megaspore in producing the female gametophyte, and the hypodermal initial thus directly produces the female gametophyte. Of course this really means that four megaspores enter into the formation of the gametophyte, and the two successive reduction divisions are the first two divisions in the formation of the gametophyte.

Female Gametophyte

Development. — The development of the female gametophyte of angiosperms begins with free nuclear division, as in gymnosperms, but the nuclei thus produced are definitely eight in number, following three successive divisions from the nucleus of the megaspore. It is in this free nuclear stage that the egg is differentiated, which is the condition of *Gnetum*, except that here the nuclei are much fewer in number. In



Figs. 589–591. — Development of female gametophyte of angiosperms, as shown by a lily: 589, megaspore (in the ovule); 590, first division; 591, second division.

connection with these free nuclear divisions two remarkable features appear. One is the polarity exhibited by the nuclei. After the first division the two nuclei separate and pass to the poles of the embryo sac, one to the micropylar end, and the other to the antipodal end (fig. 590). There follow two successive divisions, so that first two (fig. 591) and then four (fig. 592) nuclei are produced at each pole of the sac. The other

feature referred to is the *polar fusion*, which means that a nucleus from each end passes toward the center of the sac, where the two come into contact and fuse (figs. 593, 594), forming the *fusion nucleus* (primary endosperm nucleus).

Egg apparatus and antipodals. — The three nuclei in the micropylar end of the sac are organized into a group of three naked cells called the *egg apparatus* (figs. 593, 594). The cells are all potential eggs, but only one of them (the central one) matures as a functional egg. The other two are called *synergids* (helpers), because they are apparently of some service in connection with fertilization. Often the synergids become beaked, the beaks sometimes even extending into the micropyle. The three nuclei at the antipodal end of the sac form a group of three naked cells or walled cells, called *antipodal cells* (figs. 593, 594), or merely *antipodals*, and their history is exceedingly variable. Usually they are ephemeral; sometimes they are quite persistent; and in some cases they form a very active tissue. In the last case, the activity is shown either by the great enlargement of the three cells, or by their division to form a variable amount of tissue. In any case, when the antipodals are active, they serve as nutritive cells, and in general they serve this purpose until the endosperm is formed.

FIGS. 592, 593. — Development of female gametophyte of angiosperms, continued from fig. 591: 592, third division, resulting in four nuclei in each end of the sac; 593, organization of egg apparatus (upper end of sac), fusion of polar nuclei (center of sac), and antipodal nuclei (base of sac).

Exceptions. — The sequence of events described above is remarkably uniform for so great a group as the angiosperms; but there are certain interesting exceptions. For example, in a member of the pepper family

(*Peperomia*) there are sixteen free nuclei in the embryo sac. These nuclei show no polarity, and a large number of the nuclei enter into the formation of the large fusion nucleus, which in this case is the result of multiple fusion. This same general condition has been found also in *Juglans* (walnuts), *Ulmus* (elms), the aroids, etc.; but probably in all these cases two or four megaspore nuclei are involved.

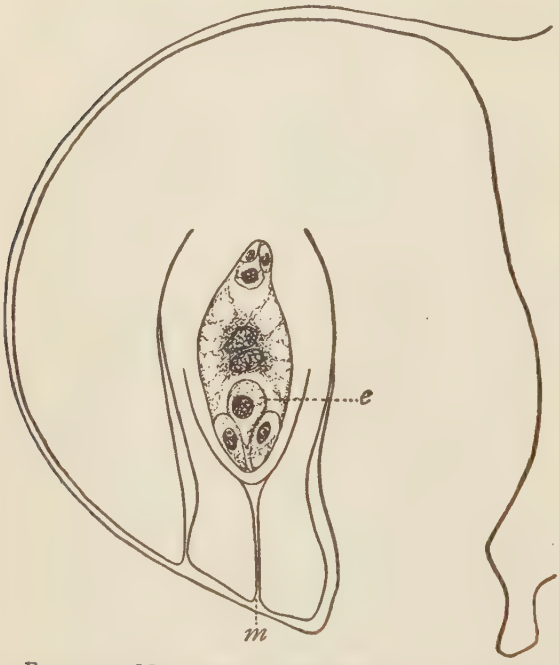
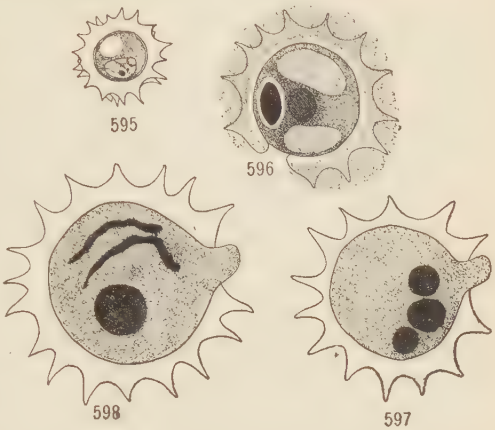


FIG. 594. — Mature female gametophyte of lily within the anatropous ovule, showing the egg apparatus (*e*, the egg; the two other cells the synergids) directed towards the micropyle (*m*), the three antipodals at the other end of the sac, and the two polar nuclei in contact in the center. — After COULTER.

Nutritive mechanism. — The nutritive mechanism of the embryo sac is varied and sometimes complex. In all cases there is an enlargement of the sac, which encroaches in every direction upon the adjacent tissue of the nucellus, which is thus used as a nutritive tissue. In some cases, notably among the Sympetalae, there is organized about the sac a definite nutritive jacket, which obtains food from the surrounding tissue and from which it enters the embryo sac. In other cases the antipodal end of the sac extends into the tissue beneath (*chalaza*), sometimes becoming conspicuously tubular and prolonged. In still other cases tubular extensions of the sac are put out in other directions, especially into the heavy integument from the micropylar end. Occasionally all of these methods of nutrition are combined, resulting in a complicated and very efficient nutritive mechanism.

Male Gametophyte

Development. — In the development of the male gametophyte of angiosperms no vegetative cell appears (except in very rare cases), so that the gametophyte is reduced to an antheridium, and the pollen grain is an antheridium initial (fig. 595). The first division of the nucleus of the microspore produces the generative and tube nuclei, and this is the usual condition of the pollen grain at shedding (fig. 596). The generative cell is usually organized as a naked cell, which assumes various forms, generally from spherical to lens-shaped. This cell may divide before the shedding of the pollen grain, in which case three nuclei are observed within the mature grains (fig. 597); or it divides after passing into the pollen tube. The generative cell is the primary spermatogenous cell, and there is only one division, resulting in two equal male cells.



Figs. 595–598. — Male gametophyte of angiosperms, as shown by *Silphium:* 595, pollen grain, with its single nucleus and spiny outer coat; 596, first division, forming generative and tube nuclei (shedding condition in many cases); 597, second (and last) division, resulting in the two male cells from the generative cell (shedding condition in some cases), a division which often occurs in the pollen tube; 598, the two male cells having elongated. — After Merrell.

The gradual reduction in the number of spermatogenous cells produced by the antheridium of a heterosporous plant has reached its extreme expression among angiosperms. In *Selaginella* the generative (primary spermatogenous) cell produces a large number of mother cells, each of which produces a sperm. In *Isoetes* the generative cell produces four mother cells, each of which develops a sperm. In cycads and *Ginkgo* the generative cell produces three cells (by two successive divisions), two of which are mother cells developing sperms. In conifers the generative cells produce the same number and character of cells as in cycads, but the two mother cells do not develop sperms, functioning

themselves as male cells. In angiosperms there is only one division, the generative cell producing two male cells. These male cells are variable in form, being spherical, lens-shaped (very common), spindle-form, curved, or even spirally twisted.

Fertilization

Pollination. — Pollination is the transfer of pollen from stamen to stigma, and is a necessary antecedent to fertilization. The term *fertilization* is often used when pollination is meant, but no student of morphology should confuse the two. In angiosperms pollination is a very extensive subject, for insects as well as wind are agents of transfer; in other words, they are insect-pollinated as well as wind-pollinated. This use of insects, which has developed among the higher angiosperms, has involved a variety of mechanism and of habit that is fairly bewildering; but the whole subject lies within the domain of ecology (see Part III). It is sufficient to note that in some cases the pollen is transferred to the stigma of its own flower (*close pollination*), and in other cases to the stigma of another flower (*cross pollination*). Dioecious plants are necessarily cross pollinated. Hybrids may be produced by cross pollinating (or *crossing*) individuals belonging to different species or varieties.

Pollen tube. — After the pollen grain lodges on the stigma, the pollen tube is developed and penetrates from the stigma to the embryo sac. This involves penetration of the style, entrance into the ovarian cavity, passage along the wall of the ovarian cavity to the insertion of the ovule, passage along the ovule to the micropyle, passage through the micropyle to the tip of the nucellus, penetration of the tissue of the nucellus overlying the embryo sac, and finally penetration of the sac wall (fig. 599). The time involved in this journey holds no relation to the distance traversed. For example, in *Crocus*, with a style 6 to 10 cm. long, the time is one to three days; while in *Arum*, with a style only 2 to 3 mm. long, the time is five days. The range of time, so far as known, is from a few hours to thirteen months (in certain oaks). These long periods are found among angiosperms which are regarded as primitive (the so-called *Amentiferae*), and suggest the similar condition among gymnosperms. Among these same primitive angiosperms, also, there are found branching pollen tubes, suggestive of the old haustorial habit of the tube.

Chalazogamy. — Among the Amentiferae there also occurs the phenomenon of *chalazogamy*, which means that the pollen tube does not enter

the embryo sac by way of the micropyle, but pierces directly through the region of the ovule beneath the embryo sac (*chalaza*) and enters the embryo sac from below. Among the more familiar plants in which chalazogamy has been found are the walnuts and elms. Entrance by the micropyle is called *porogamy;* and there are other routes used by the pollen tubes of certain plants, intermediate between true chalazogamy and porogamy.

Fertilization. — After the tip of the pollen tube has entered the sac, it enlarges very much, usually destroys one of the synergids, and finally discharges the two male cells or nuclei (fig. 599). One of the male cells passes to the egg and fertilization is accomplished. The other male cell passes deeper into the sac, comes into contact with the fusion nucleus, and fuses with it. Into the structure of the primary endosperm cell (or nucleus), therefore, three nuclei have entered: an antipodal polar, a micropylar polar, and a male nucleus. This participation of both male cells in nuclear fusions in the same embryo sac has been called *double fertilization*, and it is perhaps the greatest puzzle connected with the embryo sac of angiosperms.

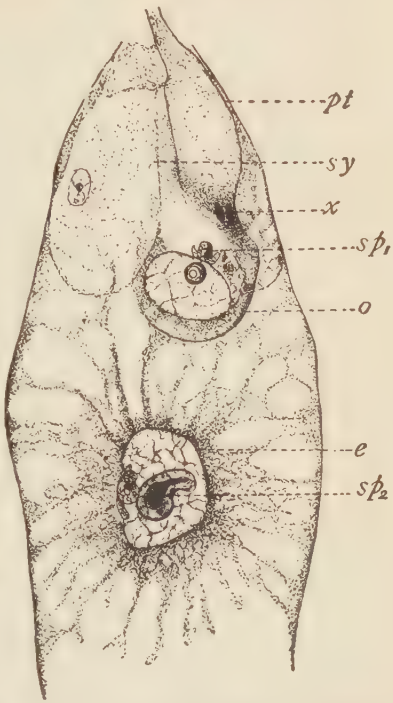


FIG. 599. — Fertilization in *Silphium:* *sy*, undestroyed synergid; *pt*, swollen tip of pollen tube, still with some contents (*x*); sp_1, coiled male cell in contact with egg nucleus (*o*); sp_2, curved male cell in contact with fusion nucleus (*e*). — After LAND.

Double fertilization. — This phenomenon was first described in 1898, but subsequent investigation has indicated that it is probably of universal occurrence among angiosperms. It means that one male cell enters into the formation of the embryo, and the other into the formation of the endosperm. This raises a question as to the nature of the endosperm of angiosperms. The old view was that it is belated tissue of the female

gametophyte, which in some way is stimulated to develop by the polar fusion. But when the part played by the male cell was discovered, it was suggested that this *triple fusion* is a real fertilization, which would mean that the so-called endosperm is a sporophyte, the twin of the embryo. If this is true, the endosperm of gymnosperms is not the same as that of angiosperms. If the test of the number of chromosomes be applied, to decide whether the endosperm is gametophytic (x) tissue or sporophytic ($2x$) tissue, it is found that it is at least $3x$ tissue. To call $3x$ tissue gametophytic seems to make the test of little value. If the triple fusion be analyzed, it will be noticed that one cell is the micropylar polar, which is sister to the egg, and another is a male cell. If only these two cells fused, it could hardly fail to be regarded as fertilization; but the third cell that enters into the fusion is a vegetative cell (or nucleus) from the antipodal end of the sac, so that the real nature of the fusion is confused. Perhaps it would be better to speak of the endosperm of gymnosperms as *female gametophyte*, and to reserve the name *endosperm* for this problematical tissue in the embryo sac of angiosperms.

Endosperm

Development. — As described above, the endosperm of angiosperms is produced by the triple fusion nucleus. It usually begins with free nuclear division, but sometimes it begins with wall formation that chambers the sac. In its completest development it forms a tissue that fills the embryo sac and is packed about the embryo. In some groups the endosperm may develop only as a few free nuclei, so that it may be regarded as suppressed, as in Helobiales and orchids (groups belonging to monocotyledons). There is also great variation in the permanency of endosperm which has been fully developed. It may be used up by the embryo during the ripening of the seed, as in peas and beans (Leguminosae); or it may persist in the mature seed, being used up by the embryo during germination, as in the cereals. In structure, permanent endosperm tissue has no intercellular spaces, and the cell wall may be thin or thick, an excessive thickening occurring in bony seeds, notably in the date and in the so-called vegetable ivory, both from the seeds of palms. Sometimes by its continued growth the endosperm has been observed to burst the seed coats, turn green, and form intercellular spaces.

Perisperm. — The storage region of some seeds is not the endosperm but the *perisperm*, which is the nucellar tissue surrounding the embryo

sac. In this case the endosperm functions as an intermediary between the perisperm and the embryo, obtaining the food stored in the former and passing it on to the latter.

Xenia.—The phenomenon known as *xenia* is the appearance in the seed of characters belonging to the pollen parent, when the pollen is foreign (belonging to another race). For example, when a race of white or yellow corn is crossed with pollen from a race of red corn, many of the resulting kernels are red or mottled. It is found that this color belongs to the endosperm, and that it is introduced by the male cell that enters into the triple fusion. This means that in this case the endosperm is a hybrid as well as the embryo.

Embryo

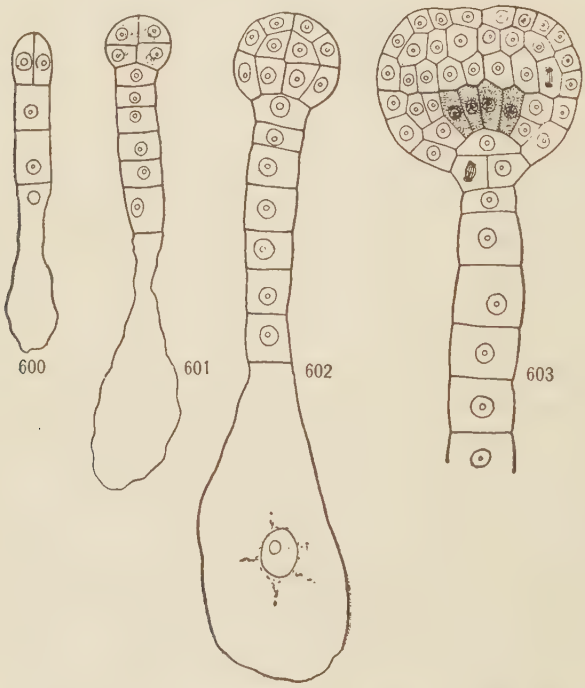
The embryo of angiosperms does not begin with free nuclear division, as in gymnosperms (*Tumboa* and *Gnetum* excepted), but the first division is accompanied by a wall. As the most fundamental difference between dicotyledons and monocotyledons is found in the embryo, the two groups must be considered separately.

Dicotyledons.—The embryo of *Capsella* (shepherd's purse) is most commonly used as a representative of the dicotyledonous embryo. The egg divides transversely and subsequent tranverse divisions result in a filament of varying length (fig. 600). This filament is the *proembryo*, which later becomes differentiated into suspensor and embryo. The terminal cell of the proembryo divides into octants (fig. 601), the four terminal octants forming the stem and cotyledons, the four basal octants forming the hypocotyl except its tip. In the octant stage the dermatogen (the layer that produces the epidermis) is cut off by periclinal walls (fig. 602). In the interior the two other body regions are soon outlined, the periblem (producing the cortex) and the plerome (producing the stele) (fig. 603).

At the tip of the hypocotyl the plerome is complete, but the periblem and dermatogen are incomplete (fig. 603). This gap in the tip of the hypocotyl is filled by the adjacent (second) cell of the proembryo as follows: This cell divides transversely, and the daughter cell next to the embryo is the *hypophysis*, which fills out the hypocotyl. The hypophysis divides transversely, the inner cells completing the periblem, and the outer cells completing the dermatogen (figs. 603–608). The second cell of the proembryo, therefore, contributes both to the embryo and to the suspensor, and the boundary between these two regions is

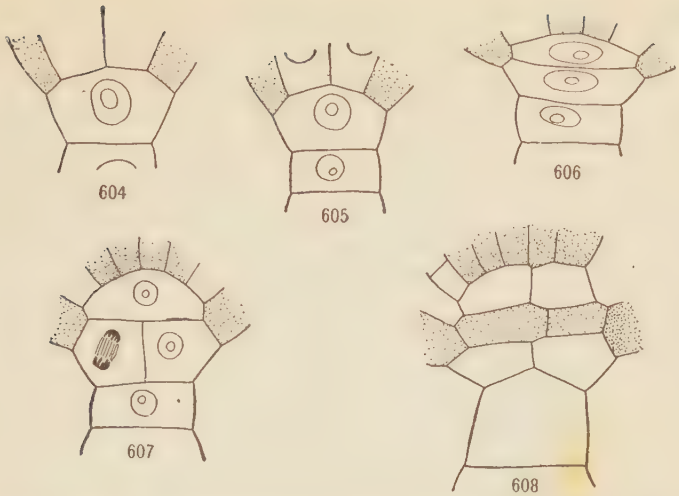
established when that cell divides and forms the hypophysis. While this method of embryo formation may be regarded as characteristic of dicotyledons, there are numerous variations, conspicuous among which are the following:

Variations. — The proembryo may be a spherical mass of cells (as in the water lilies), in which the growing points are organized, but with little or no differentiation of a suspensor.

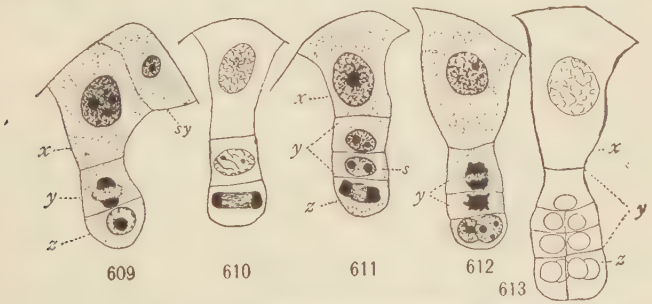


FIGS. 600–603. — Development of embryo of *Capsella* (a dicotyledon): 600, the filamentous proembryo, in which the terminal cell has divided and the basal cell has become large; 601, later stage, in which the terminal cell has divided to octants; 602, later stage, in which the dermatogen has been cut off; 603, later stage, in which plerome (shaded) and periblem (between plerome and dermatogen) are distinguishable in the hypocotyl region; hypophysis (divided to three cells in the figure) completing periblem (by inner cell) and dermatogen (by two outer cells). — After COULTER and CHAMBERLAIN.

In other cases the proembryo is massive, but of no definite form, filling the micropylar end of the embryo sac.



FIGS. 604–608. — The hypophysis in *Capsella:* 604, cell with nucleus is the cell of the filamentous proembryo next to the terminal one (which has formed most of the embryo); 605, division of this cell into hypophysis (cell next to the embryo) and end cell of suspensor (it is this division that finally differentiates embryo and suspensor); 606, division of hypophysis into two cells; 607, division of the outer daughter cell of the hypophysis; 608, final product of the hypophysis (six cells visible, in three tiers), innermost tier completing the periblem (plerome shaded), middle tier (shaded) completing the dermatogen (shaded), and outermost tier starting the root cap. — After COULTER and CHAMBERLAIN.

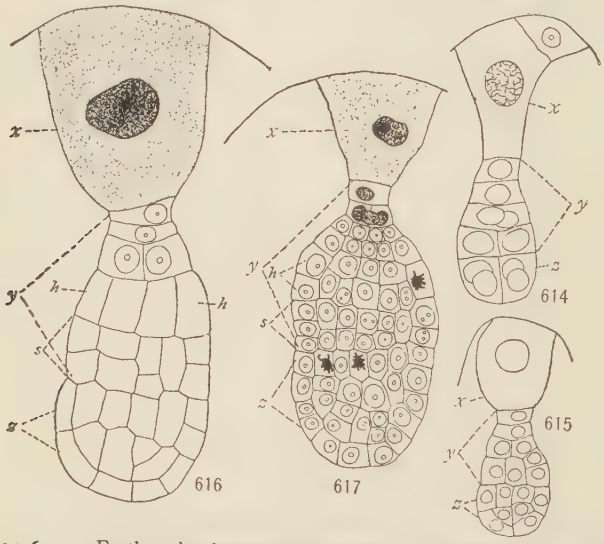


FIGS. 609–613. — Development of embryo of *Sagittaria* (a monocotyledon): 609, the three-celled filamentous proembryo, the terminal one (*z*) forming the cotyledon (*sy*, the undestroyed synergid); 610, the same; 611, division of middle cell; 612, 613, later stages; *x*, enlarged basal suspensor cell; *y*, middle cell; *z*, terminal cell. — After SCHAFFNER.

Among the Leguminosae there is often developed a conspicuous and very active suspensor, which may almost girdle the sac with its turgid cells.

Among certain plants without chlorophyll (*Monotropa*, etc.) the embryo is very simply organized, consisting of a few cells, the differentiation into body regions proceeding during germination..

Monocotyledons. — The embryo of *Alisma* or of *Sagittaria* is most commonly used to represent the monocotyledonous embryo. The proembryo is usually a filament of three cells (figs. 609, 610), the terminal cell forming the cotyledon. The middle cell begins a series of divisions, some of the resulting cells forming the stem tip, hypocotyl, and root tip, and the others belonging to the suspensor (figs. 611–617). In



FIGS. 614–617. — Further development of embryo of *Sagittaria:* stages later than the series shown in figs. 609–613; *x*, enlarged basal cell; *y*, middle cell, giving rise to stem-tip (*s*), hypocotyl (*h*), and some suspensor cells; *z*, the terminal cotyledon. — After SCHAFFNER.

this case, also, the boundary between embryo and suspensor is established by a division of the second cell of the proembryo, which contributes both to the embryo and to the suspensor (fig. 617); but in this monocotyledon type the whole of the embryo except the terminal cotyledon is derived from the second cell. The basal cell of the proembryo usually becomes very much enlarged, forming the conspicuous part of the suspensor (figs. 616, 617). The notable monocotyledonous feature is the terminal cotyledon and the laterally developed stem tip, which appears in a notch developed in the side of the axis of the embryo (fig.

618). Notable variations in this method of embryo formation are as follows:

Variations. — Among the aroids the proembryo is usually a spherical mass of cells.

In *Lilium* and its allies the suspensor becomes massive, sometimes filling the micropylar end of the sac, and occasionally giving rise to extra embryos.

In orchids the embryo is very simply organized at the maturity of the seed, consisting of only a few cells, with no differentiation into body regions.

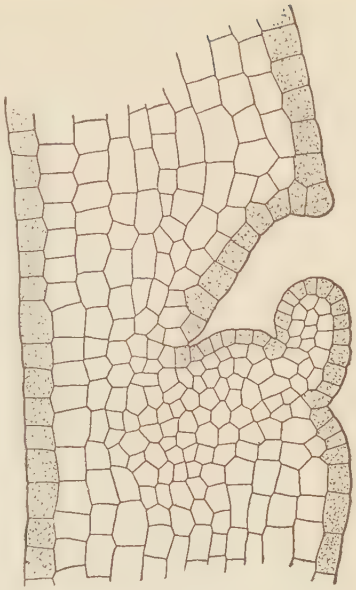


FIG. 618. — Stem tip of *Sagittaria* developing in notch on side of embryo. — After SCHAFFNER.

PARTHENOGENESIS

Parthenogenesis is the development of an embryo from an unfertilized egg, and it seems to be a rare phenomenon among angiosperms, having been recorded thus far in only six or eight scattered genera, conspicuous among which are species of *Thalictrum*, *Alchemilla*, *Antennaria*, and *Taraxacum*. In these cases, since there is no fusion of nuclei in the act of fertilization, there is no doubling of the chromosomes; but it has also been found that in them there is no reduction division in the formation of the megaspores, so that the egg already has the $2x$ number, which is transmitted to the young sporophyte (embryo).

POLYEMBRYONY

The occurrence of more than one embryo in a seed is not so common among angiosperms as among gymnosperms, but the cases are numerous. The synergids and the antipodals have been observed to produce embryos, and since these cells are gametophytic, these embryos arise by vegetative apogamy (see p. 169). Very commonly also the cells of the nucellus adjacent to the embryo sac or even those of the integument may form embryos that push into the sac. Since the nucellus and in-

tegument belong to the sporophyte, these embryos arise by sporophyte budding. A remarkable case is that of an *Allium* (onion) with five embryos in the sac: one from the fertilized egg, one from a synergid, two from the antipodals, and one from the integument. There are thus four possible ways by which embryos may appear in an embryo sac: (1) from a fertilized egg, (2) by parthenogenesis, (3) by vegetative apogamy, and (4) by sporophyte budding.

Classification of Angiosperms

In so vast a group as angiosperms, it is impossible to present so complete a classification as was given for the gymnosperms or even for the pteridophytes. However, it seems necessary to indicate the larger groupings. The scheme presented is known as that of Engler, and although it will doubtless be very much modified, it will serve to introduce the great groups.

Monocotyledons

Among Monocotyledons about 25,000 species are recognized, which are distributed among 42 families; and these families are grouped into ten great alliances. These alliances may be considered under two categories, six of them having spiral flowers (with indefinite numbers), and four of them having cyclic flowers (with definite numbers). The spiral alliances are regarded as the more primitive, and the cyclic alliances represent the more advanced monocotyledons. The six spiral alliances are as follows:

1. *Pandanales* (3 families, 100 species). — The screw pine is the representative form, but the cat-tail flag (*Typha*) is a representative in our flora. The group is regarded as low in rank, which means either that it is primitive or reduced, because it has naked flowers with indefinite numbers, and is wind-pollinated. Another noteworthy feature is that the flower cluster is protected by the sheathlike base of the leaf.

2. *Helobiales* (7 families, 235 species). — This is also an aquatic and wind-pollinated group, whose lowest members have naked flowers, as the pondweed (*Potamogeton*), but whose higher members have a calyx and corolla, as the water plantain (*Alisma*). In this group, also, the sheathing base of the leaf encloses the young flower cluster.

3. *Glumales* (2 families, 7000 species). — These are the grasses and sedges, which form one of the greatest of angiosperm alliances. While there are aquatic members, it is chiefly a terrestrial group, covering the

earth's surface more completely than any other. The flowers are naked and wind-pollinated, and the floral numbers fluctuate widely. The peculiarity of the group, which has suggested the name, is that the individual flowers are protected by bracts (*glumes*), the flower clusters being composed of these overlapping bracts. This method of protection is in strong contrast with that of the preceding groups.

The three preceding alliances are those which contain naked flowers, and if this is a primitive character, these are the most primitive alliances of the monocotyledons. It must be remembered, however, that this condition may have arisen through reduction.

4. *Palmales* (1 family, 1100 species). — These are the palms, the chief group of trees among the monocotyledons. The flowers have a perianth, but it is not differentiated into calyx and corolla. In general the floral numbers are indefinite, but there is occasional evidence of a settling to three, especially in the carpels, which are not only usually three in number, but also syncarpous. With the appearance of a perianth, there is also the appearance of insect pollination, so that the group as a whole is both wind-pollinated and insect-pollinated. It is also characterized by the large sheathing bases of the leaves, which invest the young flower clusters, a feature in common with the first two groups.

5. *Synanthales* (1 family, 45 species). — This is a small and peculiar South American alliance, which needs no description in this connection.

6. *Arales* (2 families, 1025 species). — These are the aroids, a very distinct group of monocotyledons. The best known representatives are probably Jack-in-the-pulpit (*Arisaema*) and calla lily, but numerous tropical forms are in common cultivation in greenhouses. The flowers are clustered on a fleshy axis (*spadix*), enveloping and often overarching which is a great bract (*spathe*). The spathe is as variable in form and variegated in color as are ordinary flowers, and associated with it there is a development of insect pollination. In fact, the brightly colored spathe seems to play the same part in aroids as does the corolla in the higher groups. The flowers clustered on the spadix are exceedingly variable as to the perianth; and although the stamens and carpels are indefinite in number, the number is small (1–4). A very distinct feature of aroids among monocotyledons is the production of broad, net-veined, and frequently lobed leaves, which resemble those of dicotyledons. One of the families is made up of the duckweeds (*Lemna*), which are very much reduced aquatic forms.

The preceding alliances are the so-called spiral alliances, in which the floral members are not definitely and constantly of the same number. While the floral number three is a feature of monocotyledons, it is evident that it does not apply to the spiral alliances in the same sense that it does to the cyclic alliances.

In the following cyclic alliances the almost constant floral formula is: perianth 3 + 3, stamens 3 + 3, carpels 3 (and syncarpous). Furthermore, the perianth is the conspicuous floral feature rather than bracts, and insect pollination is well established. In other words, the real flowers of monocotyledons, as ordinarily recognized, belong to the cyclic alliances.

7. *Farinales* (11 families, 2000 species). — This alliance is in a certain sense a transition group between the spiral and cyclic alliances; for although the cyclic number is established, many of the forms are grass-like herbs with bractlike perianth, as in the rushes (Juncaceae); but there are also forms with showy corolla, as the spiderwort (*Tradescantia*).

8. *Liliales* (9 families, 5000 species). — These may be regarded as the representative monocotyledons, with conspicuous and usually regular perianth, and well-established insect pollination. Most of the monocotyledonous flowers of ordinary experience belong here. The group shows a distinct development from hypogyny, as in the amaryllises (Amaryllidaceae), to epigyny, as in the flags (Iridaceae).

The two remaining cyclic alliances are characterized not only by epigyny, but also by the extreme irregularity of the flowers.

9. *Scitaminales* (4 families, 800 species). — These are the cannas, bananas, and gingers of the tropics. One peculiar feature of the group is the so-called false stem, which may be seen in the banana. The stem-like structure, which often rises to a considerable height, is built up of the heavy and overlapping bases of the leaves.

10. *Orchidales* (2 families, 7000 species). — The orchids are notable for the great irregularity and showiness of their flowers, and for their extreme specialization in insect pollination. The number of species runs very high, but orchids cannot be regarded as abundant. By contrasting the 7000 species of grasses and sedges with the 7000 species of orchids, it becomes evident that although the species of two groups may number the same, the number of individuals may be very different. The orchids may be regarded as the culmination of monocotyledons in floral structure, and that culmination is expressed by epigyny and extreme irregularity.

Archichlamydeae

This vast group contains a maze of forms whose relationships are very confusing. Over 61,000 species and 180 families are recognized, which are grouped into 26 great alliances. Archichlamydeae include primitive angiosperms, and although they are prevailingly spiral, the cyclic condition, with a definite number in all of the floral members, is established in several of the higher alliances. It would be unprofitable to name all of the alliances, for many of them would suggest nothing to the elementary student. Some of the more significant will be selected for brief description, and the others grouped.

1–12. (26 families, 5900 species.) —This group of alliances is especially puzzling as to relationships. They are regarded as relatively primitive forms, and include many of the most common trees, as willows, walnuts, beeches, oaks, etc. Many of them were formerly grouped as Amentiferae, a name referring to the characteristic flower cluster called *ament* or *catkin*, a cluster perhaps most familiar in the willows and alders. The flowers are naked or have a bractlike perianth, the floral numbers are generally indefinite, and wind pollination prevails. This assemblage does not seem to be related to any of the higher alliances.

13, 14. (11 families, 4070 species.) —This is another apparently isolated group, including such plants as smartweed (*Polygonum*), pigweed (*Amaranthus* and *Chenopodium*), pinks (Caryophyllaceae), etc. In structure the flowers range from a bractlike perianth to distinct sepals and petals, and are mostly cyclic, three, four, and five being the prevailing floral numbers. Insect pollination is established only among the pinks.

15. *Ranales* (16 families, 4050 species). —This is recognized as the great genetic alliance, which means that the higher alliances are thought to have been derived from it. Familiar families are the crowfoots or buttercups (Ranunculaceae), the water lilies (Nymphaeaceae), and the magnolias (Magnoliaceae). There is a distinct calyx and corolla; the flowers are hypogynous; and the numerous carpels form separate pistils (*apocarpous*). Although the cyclic number is often evident in the calyx and corolla, the stamens and carpels at least usually retain the spiral condition and are indefinitely numerous. By some it is thought that the Ranales are the most primitive Archichlamydeae, not only giving rise to the other dicotyledons, but also to the monocotyledons.

16, 17. (9 families, 2760 species.) — These families are clearly special branches from Ranales, the most specialized one probably being the mustards (Cruciferae).

18. *Rosales* (16 families, 14,270 species). — This is the greatest alliance among the Archichlamydeae, including far the largest family — the Leguminosae, with over 11,000 species. Another prominent family is the Rosaceae, which gives name to the alliance. These two families are plainly branches from the Ranales; and among the Leguminosae the flowers become conspicuously irregular. The irregularity is of a special type, illustrated by the sweet pea, so that a large part of the family is easily recognized. In the development of irregularity in connection with insect pollination, the Leguminosae hold the same position among Archichlamydeae that the orchids (Orchidaceae) hold among monocotyledons.

19–25. (99 families, 27,358 species.) — This is a tangle of seven alliances leading off in every direction from the preceding ones, each alliance characterized by some special feature. Each one, however, gradually becomes more definitely cyclic and approaches the epigynous condition.

26. *Umbellales* (3 families, 2660 species). — This is easily the highest of the alliances of Archichlamydeae and it is kept from being included among the higher Sympetalae only because it is polypetalous. The dominant family is the parsley family (Umbelliferae), and associated with it are the dogwoods (Cornaceae). The floral formula is definitely as follows: sepals 5, petals 5, stamens 5, carpels 2, and this is also the most advanced floral formula found among Sympetalae. Associated with this high formula is epigyny. Another high character is that the flowers are small and massed, the cluster being more or less invested by a rosette of bracts (*involucre*). Apparently as a result of the massing of the flowers, the sepals are much reduced, and the whole cluster shows more or less division of labor, some flowers (the peripheral ones) often being more showy, and the others more fertile.

Sympetalae

This is a much better defined group than the Archichlamydeae, from which they are certainly derived. The combination of characters is as follows: completely cyclic flower, sympetalous corolla, ovule with a single massive integument, and complete absence of wall tissue in the ovule (see p. 263). About 42,000 species and 51 families are recog-

nized, which are grouped into eight alliances, whose characters and sequence are quite evident.

The first three alliances are called the *pentacyclic* and *isocarpic* alliances. The former term means that there are five cycles of floral members, the stamens being in two cycles; the latter term means that the number of carpels is the same as that of other cycles. The floral formula which expressses both of these facts is as follows: sepals 5, petals 5, stamens 5 + 5, carpels 5 (syncarpous). These pentacyclic Sympetalae are most nearly related to the Archichlamydeae, and in fact contain some polypetalous forms. They are not very numerous, including only about 3500 species.

1. *Ericales* (6 families, 1700 species). — The heaths constitute the dominant family (Ericaceae), very characteristic of northern latitudes. Some of the forms are polypetalous, but they are so related to sympetalous forms that they cannot be separated from them; and in some of the sympetalous forms the stamens are free from the corolla. One of the features of the alliance is the characteristic dehiscence of the anthers, which is by means of terminal openings in the tubular prolongations of the pollen sacs.

2. *Primulales* (3 families, 850 species). — Two features of this alliance, of which the primroses (Primulaceae) are representatives, are the opposite stamens and free central placenta. The five stamens are opposite the five petals, instead of alternate with them, as is usual; but this is explained when it is discovered that the outer cycle of stamens is abortive, being represented by rudiments called *staminodia*. The axis of the flower extends into the ovary cavity like a central column, and upon it the cauline ovules are developed, a condition which was formerly called free central placentation.

3. *Ebenales* (4 families, 900 spec es). — These are mostly tropical shrubs and trees, represented in our flora by the persimmon (*Diospyros*). As the name suggests, the characteristic family is the ebony family (Ebenaceae). It is a curious mixture of primitive and advanced characters, with frequent lapses into indefinite numbers, especially of stamens.

The remaining alliances are *tetracyclic* and *anisocarpic*. This means that there are usually only four floral cycles, and that the number of carpels is not equal to that of the other cycles. The general floral formula is as follows: sepals 5, petals 5, stamens 5, carpels 2 (syncarpous). In the more primitive alliances the carpels fluctuate between five and two, often being four or three. The five tetracyclic alliances fall naturally into

two groups, the first three having hypogynous flowers, and the other two having epigynous flowers. The hypogynous alliances are as follows :

4. *Gentianales* (6 families, 4200 species). — The combination of characters that distinguishes this alliance from the next is the uniformly opposite leaves and twisted *aestivation* (petals in the bud appearing as if twisted around each other). As the name suggests, the gentian family (Gentianaceae) is the characteristic representative of the alliance. The curious and highly specialized milkweeds (Asclepiadaceae) are also included here, characterized not only by their milky juice, but chiefly by their elaborately insect-pollinated flowers and pollinia (see p. 258).

5. *Tubiflorales* (20 families, 14,600 species). — This great alliance represents the culmination of the hypogynous Sympetalae, with conspicuous tubular corollas. The flowers range from regularity, as in the morning glories (*Ipomoea*) and polemoniums (Polemoniaceae), to irregularity, as in the mints (Labiatae) and figworts (Scrophulariaceae). The type of irregularity in this case is called *bilabiate*, which means that the corolla develops a two-lipped mouth. These Tubiflorales with irregular flowers hold the same position in reference to insect pollination among Sympetalae that the Leguminosae do among Archichlamydeae, and the Orchidaceae among monocotyledons.

6. *Plantaginales* (1 family, 200 species). — This small alliance, comprising the single family of plantains (Plantaginaceae), is characterized by flowers with a membranous corolla and the cyclic number four. Its relationships are obscure, but it is probably a reduction group.

The two following epigynous alliances represent the culmination of Sympetalae, and therefore of angiosperms.

7. *Rubiales* (5 families, 4800 species). — The madders constitute the characteristic family (Rubiaceae), and associated with it are the honeysuckles (Caprifoliaceae). The cyclic number is prevailingly four, and there is a strong tendency to aggregate the flowers in close clusters.

8. *Campanales* (6 families, 14,500 species). — This highest alliance is dominated by the great family Compositae (sunflowers, asters, goldenrods, dandelions, etc.), which is not only the highest, but the greatest of angiosperm families, including at least 12,500 species. It adds to its sympetaly epigny, a seedlike fruit (*achene*), a special development of its sepals as *pappus*, a complex organization of flowers into a head so compact as to simulate a single flower, and usually a differentiation of the flowers of a head into those that are showy (the peripheral *ray flowers*) and those that are fertile (*disk flowers*).

CHAPTER V — ORGANIC EVOLUTION

THE morphology of plants, as presented in the preceding chapters, is in reality a somewhat detailed illustration of the evolution of the plant kingdom. The theory of descent is the working theory of modern biology, and no student of morphology should omit some consideration of it. The subject has developed so extensively that it can be presented here only in very brief outline, an outline that may serve as an extended definition, and also as an introduction to a real study of organic evolution. Many names connected with the doctrine of evolution and many important views in reference to it must be passed over, and only the most conspicuous features presented.

Definition. — The doctrine of organic evolution claims that the existing plants and animals are the modified descendants of earlier forms; that in some way new forms have arisen from the old ones, and have given rise in turn to still other forms. According to this view, the whole plant kingdom, for example, may be likened to a profusely branching tree, the tips of whose myriad branchlets represent our present flora. The morphologist attempts to trace these branchlets from their tips, which he sees, to their connections, which he can only infer. His proofs are obtained from the structure and development and behavior of living plants, and also from the form and structure of ancient plants, so far as they are available in suitable fossil form. His conclusions, it must be remembered, are reasonable inferences, and cannot be based upon actual demonstrations. It is evident that opinions may differ widely as to the actual historical connections of plant groups; but it is practically unanimous that there are such connections.

The idea of organic evolution is not modern, being in the thought of man as far back as records of thought have been found; but it is only in modern times that it has been based upon direct observation of the facts, that is, has become scientific. It is not necessary to recite the facts that underlie the widespread belief in organic evolution, for many of these facts, so far as they concern plants, have been given in the preceding chapters. To believe in organic evolution, however, is one

thing, and to explain it is a very different thing. The well-known names associated with the doctrine of evolution often are thought of as the names of men who may be called authors of the theory of evolution; but they are really men who have proposed explanations of evolution. For example, Darwin, perhaps more than any other evolutionist, is spoken of as the author of the doctrine of organic evolution; but if his explanation and every other explanation should be disproved, the fact of evolution would still remain to be explained. No proposed explanation of evolution is entirely satisfactory, but biologists are daily becoming more convinced of the truth of evolution.

With this distinction between the fact of evolution and its explanation made clear, it will be possible to outline briefly the conspicuous explanations that have been offered. The problem to be solved is how new forms may arise from old ones, which is the problem of the origin of species.

Environment. — Perhaps the oldest explanation of organic evolution, based upon observation, is that plants and animals may be changed by their environment. Such facts as the seasonal changes in the plumage of birds and in the covering of mammals, and also the changes in plants in relation to their environment, suggested that plants and animals are plastic and can be molded by a changing environment. This explanation was offered, during the last decade of the eighteenth century, by Erasmus Darwin of England, St. Hilaire of France, and Goethe of Germany. It was assumed that any change induced by environment would be transmitted to the offspring, to be retained so long as the environment remained constant.

It is evident that organisms respond more or less in certain ways to decided changes in the environment, but such direct responses are regarded generally as too superficial and fluctuating to account for the production of new forms. The influence of environment, however, while insufficient to explain organic evolution, is still recognized as an important factor of the problem, whose value may vary widely. If there are such things as "ecological species," their origin is due by definition to environment.

Use and disuse. — In the early part of the nineteenth century, Lamarck offered an explanation of evolution, which he called "appetency," meaning the effect of desire. The theory is better known as Lamarckism, and it has strong defenders, in modified form, to the present day. It is really the effect of use and disuse. It is well known that persistent

use develops such an organ as a muscle, and that persistent disuse causes it to dwindle and to lose its power of functioning, leading eventually perhaps to abortion or even to suppression. If this law is conceived of as applying to every organ of a plant or an animal, the results might be as deep-seated and general as could be demanded by the origin of new forms.

According to this theory, the use or disuse of an organ is determined by the environment. A change in the environment might shift the demands upon the different organs, and so build up or modify some and allow others to degenerate, resulting in a different kind of plant or animal. This process is sometimes called " adaptation," the idea being that plants and animals can " adapt " themselves to fit their environment. Lamarck used the neck of the giraffe as one of the striking illustrations of his theory. He imagined that a grazing animal, thrust into an environment where feeding upon the foliage of trees became more or less necessary, would call upon its neck in such a way that it would become somewhat elongated; and that the gain in length secured by any individual would be transmitted to its offspring, so that generations of such animals would gradually build up the enormously elongated neck of the modern giraffe. Such a result would mean the transmission of small changes acquired during the lifetime of an individual, and the possibility of such transmission is now generally disbelieved.

The three factors recognized by this theory are (1) a changing environment, (2) the effect of use and disuse, and (3) the inheritance of acquired characters. The first two factors are evidently important, but they are of no avail in producing new forms, according to Lamarck, unless the third factor operates.

Natural selection. — The explanation of organic evolution by means of natural selection is more widely known than any other evolutionary theory. Its announcement in 1858 by Charles Darwin and the appearance in 1859 of his book entitled *Origin of species by means of natural selection* introduced a new epoch in scientific thought and method. Modern biology, in a very real sense, may be said to date from this book, and what is called Darwinism has dominated it for nearly fifty years. The enormous mass of facts, obtained from world-wide observations and prolonged experiments, was organized in such a convincing way to support the theory that only wider observation and more careful experiment could make it appear unsatisfactory. In fact, the theory of natural selection as presented by Darwin led to a wide acceptance of

the doctrine of evolution. Whether the theory stands or falls as an explanation of the origin of species, its supreme importance in the history of biology demands that it be understood by all students of plants and animals. The bare outline of the theory is as follows:

The theoretical "ratio of increase" of plants and animals is far beyond their actual increase. If an annual plant should produce two seeds, and each seed should "fulfill its mission," there would be two plants in the second season, four in the third, eight in the fourth, and so on in geometrical ratio, until in comparatively few years there would be many millions of descendants from a single individual, enough to populate the whole earth. If this ratio of increase be applied to the myriads of plants and animals of many kinds, the result would be a tremendous competition for space and food, a competition which has been called "the struggle for existence." Since in general the number of adult plants and animals is no greater in one season than in the preceding, it is evident that the "struggle" results in a tremendous destruction of individuals. This leads to the striking conclusion that "death is the rule, and life the exception."

In considering this enormous waste of living forms, Darwin concluded that the survivors of the "struggle" must be better situated or equipped than their less fortunate fellows, and that the competition resulted in what Spencer afterwards called "the survival of the fittest," which is another way of saying "the destruction of the unfit."

The idea that two plants from the same parent might be differently equipped, led to the observation of the facts of variation. No two individuals of the same species, even from the same parent, are alike in every detail; and the variations range from very minute ones to very large and striking ones. It was concluded that there must be a selection from among these variants of those best suited to the conditions of living. There was no attempt at this time to search for the cause of variation; it was simply accepted as a fact which makes evolution possible.

The actual demonstration of the use that can be made of variations was obtained by Darwin from the operations of plant and animal breeders, who had long changed plants and animals under domestication. Some of these changes had been so extensive that it was difficult to believe that the wild form and the highly cultivated form were the same species. In fact, had they both been found growing wild they would probably have been described as two species. The process of the breeders was to select from the variants those which best suited their

purpose, and to continue this selection generation after generation. It was found that this continuous selection gradually built up the selected characters, until the desired result was obtained. This could well be called the origin of new forms by artificial selection; that is, selection directed by man.

Darwin concluded that there is a process similar to this going on in nature. Innumerable variants are constantly appearing, in numbers beyond any possibility of their continuance. The more suitable ones are selected by nature for survival, the means of selection being "the struggle for existence." This selection continuing from generation to generation, the favorable variations would be perpetuated and increased, and eventually the variation might become so great that it could be regarded as standing for a new species. The very appropriate name given to this process is natural selection, and its method consists in the slow building up of small variations, in a given direction determined by the environment, to one great enough to cross the boundary of the parent species.

Although natural selection is certainly operative in the destruction of certain forms and the preservation of others, it is thought by many to be doubtful whether this process can result in the production of new species. Some of the reasons for this doubt that have been urged are as follows:

(1) It is generally believed that acquired characters are not inherited; and if so, it is thought that the small variations exhibited by individuals would not be passed on to their progeny with any certainty. An acquired character is one that is "taken on" by the individual during its lifetime, and is no part of its parental inheritance. The variations claimed to be used by natural selection, however, are probably inherited for the most part, and can hardly be included among acquired characters; so that this objection is not a serious one.

(2) It is claimed that the slight variations used by the theory of natural selection cannot be extended by continuous selection beyond the boundary of the species; in other words, that there is a limit of variation for each species, which cannot be passed by variations of this type. Such variations are commonly spoken of as fluctuating variations, and the amount of fluctuation varies in different species. It is claimed that with all the centuries of artificial selection by plant and animal breeders, the species boundary has never been crossed by this process.

(3) It is recognized that the forms improved by artificial selection

are inconstant. If a plant which has been built up in certain characters by culture be left to nature, it reverts or "runs back," and its descendants soon lose the characters of cultivation and resume those of the ancestral stock. It is evident that the establishment of a new species demands constancy in the built-up characters. The only answer to this objection is that the characters for which man selects are not those for which nature selects; and therefore the inconstancy in nature of a plant built up by culture is no proof that a plant built up by natural selection would be inconstant in nature.

(4) It is also urged that many forms and organs continue to exist which are in no sense "adapted." If nature is selecting suitable individuals and organs, that is, those "adapted" to their environment, and is destroying those that are not, why do so many of the latter survive? There are so many cases of this kind, that the selection by nature does not seem to be based upon the suitability of an individual or an organ.

(5) Perhaps the most serious objection to the theory is that it demands a selection among such slight variations that one can hardly be conceived of as having any decided advantage over another, really a "life and death advantage." If broad leaves are of advantage to a certain species growing under certain conditions, selection among individuals with broad and narrow leaves would seem to be easy; but the theory demands that the selection be made before the broad leaves are built up, and continue during the slow process of building. In other words, the advantage given by a completed structure is not evident during the process of building up; but natural selection is supposed to be directing this building up on the basis of a distinct advantage from generation to generation. To select among completely equipped individuals is one thing; but to select so that individuals may become equipped is a very different thing.

Mutation. — In 1901 Hugo DeVries offered an explanation of the origin of species, which he called mutation. He had observed in one of the few vacant fields in Holland an evening primrose (*Oenothera Lamarckiana*), which had been introduced from the United States. Among the numerous individuals he found some so unlike the ordinary form that he was compelled to regard them as distinct species, and inquiry showed that they had never been described. Plants of *O. Lamarckiana* and of the new species were removed to the garden at Amsterdam and studied through many generations.

It was found that when thousands of seeds of *O. Lamarckiana* were

germinated, there would appear among the seedlings a few that were very different from the others. These few being brought under cultivation developed into individuals with all the marks of species distinct from the parent. Moreover, they "came true," generation after generation, which is regarded as the final test of a species. In this way *O. Lamarckiana* was observed to give rise to several new species, in some cases the same species appearing repeatedly. Not all of these suddenly produced species would have survived in nature, but some of them had already stood this test in the vacant field. This immediate appearance of a fully equipped new species, without any intermediate stages or any building up by selection, DeVries called *mutation*, the forms thus produced being *mutants*. The rôle of natural selection in this case is not to produce species, but to select among those already produced. It is evident that a mutant is simply a large variation, such as are called "sports."

DeVries investigated the results of plant breeders, as Darwin had done, and distinguished between improved forms and really new forms. The former evidently arose from the continuous selection of small variations, and were always inconstant. The very few new forms produced were constant, and, so far as records of their pedigree were available, were found to have arisen in each case from some individual that had suddenly appeared among the cultures. In other words, new forms were found, not produced; and when found, they remained constant. Naturally DeVries concluded that all the new and permanent forms that have appeared in connection with plant breeding have been mutants, and have not been built up by continuous selection.

It is entirely unknown whether this mutating condition is of general occurrence. Cultures of plants and animals are being carried on by numerous investigators, and the results may indicate presently whether mutation is to be regarded as a general method in the origin of species or as only an occasional one. It is becoming more and more evident that new species may have arisen in several ways, perhaps including all the methods heretofore suggested, and certainly including some that remain to be discovered. Whether mutation stands or falls as an explanation of evolution, the most important contribution of DeVries to evolutionary science is its transfer from the field of observation and comparison to the field of experimental work.

Orthogenesis. — Natural selection utilizes small variations in building up new species, and mutation calls large variations species. In both

cases the parent organism is supposed to give rise to progeny that vary in every direction, the successful direction to be determined by natural selection. This has been called indeterminate variation. In tracing the evolution of great groups, however, it becomes clear that the important variations occur in certain definite directions, which have been maintained persistently throughout all possible changes of condition. For example, the history of such a group as gymnosperms shows a tendency to vary in certain definite directions that has persisted from the early Paleozoic to the present time. What is true of the tendencies that result in great groups, has also been found to be true in many cases of related species. In other words, there is much to indicate that while variation may be indeterminate, there are also certain definite and predetermined lines that persist. This origin of new forms (whether by natural selection or mutation or neither), as the result of a persistent determinate variation, is called *orthogenesis*. It certainly removes one of the greatest difficulties in the way of natural selection, and that is the beginning and development of a structure that can be of advantage only when completed. It satisfies also the many known cases of excessive development in certain directions, a development that may be not only disadvantageous, but even destructive.

Even if determinate variation is accepted as a fact, however, what determines the persistent variation? The answer to this question has resulted in many variations of the theory of orthogenesis. In the earlier development of the theory, it was perhaps natural to explain it by means of a mysterious principle inherent in organic life, "an inner directive force" that persistently makes for progress. Of course such an "explanation" could not satisfy modern biologists, who prefer to believe that determinate variation is occasioned by external factors; but it is still very uncertain how these external factors operate, and even what they are.

It should be noted that natural selection, mutation, and orthogenesis are not mutually destructive. They all deal with variations, and may all be operative in producing new forms. Natural selection deals with fluctuating variations, which are small and in every direction; mutation with large variations, which are large and in every direction; and orthogenesis with those small or large and relatively few variations which for some reason persist and increase from generation to generation and carry forward the group as a whole.

Weismannism. — The theories of Weismann have strongly favored Darwin's theory of natural selection by supporting it at its weakest points.

The theory of *panmixia* attempts to explain how organs degenerate, which natural selection cannot explain unless the abandoned organs are injurious. Natural selection is assumed to select favorable structures and make them still more favorable, but not to eliminate structures that have simply become useless. According to Weismann, when selection ceases to operate upon a certain organ because it has become useless under new conditions, individuals with this organ poorly developed will no longer be at a disadvantage and therefore will survive. The crossing of individuals with this organ in all stages of effectiveness will result in the next generation in lowering the general level of efficiency, and the organ as a whole will appear degenerate. This general mixing, which lowers the average of efficiency, is called *panmixia*. It is impossible to explain, however, how panmixia could lead to a continuous degeneration of the organ involved.

Weismann's theory of *germinal selection* (1895) is one of the most ingenious speculative explanations of the beginnings of variation and of determinate variation (orthogenesis) that has been proposed, neither of which natural selection seemed able to explain, for it can operate only upon variations that have been carried forward to the point of distinct advantage, and it cannot carry forward a variation in spite of changing conditions. Weismann differentiated between *somatic* protoplasts, which give rise only to the vegetative cells of the plant or animal body, and *germ* protoplasts ("germ-plasm"), which give rise to the reproductive cells. The nuclei of the protoplasts contain large numbers of imaginary living units (*biophores*), and these units are organized into groups (*determinants*) which determine the character of the cell. Each kind of somatic cell is supposed to be produced by a certain kind of determinant; but a germ cell contains all the determinants that belong to all the cells of the body. The structure of the offspring depends upon the determinants that are favored in development, and this at first seems to be a matter of chance in food supply. There results a "struggle" among determinants, and a "germinal selection." The stronger determinants that become established in the germ-plasm, however, are handed down generation after generation, and therefore a variation once begun may continue until it can be laid hold of by natural selection, or may even continue as the persistent determinate variation recognized by orthogenesis.

Ingenious as this explanation is, it must be stated that it rests upon no demonstration, and that there are serious objections to it.

Isolation. — The importance of isolation in the formation of species is variously estimated, but that it is at least of great assistance seems evident to those best acquainted with species in nature. If a group of individuals possessing a certain variation were associated with a larger number of closely related individuals not possessing it, the intercrossing of the two groups might obliterate the distinction. On the other hand, if the varying group were isolated from all of its near relatives, so that there could be no intercrossing, the variation would be far more likely to persist and increase. In other words, a variation that otherwise might disappear may be established by isolation.

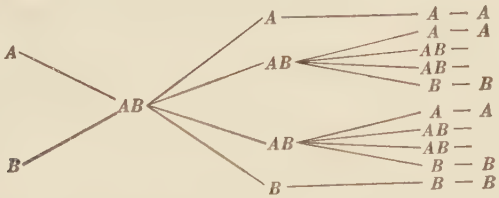
The term *isolation* usually suggests geographical or topographical isolation, which is perhaps the most effective kind. Migration distributes individuals widely, and the various barriers that segregate them into distinct groups are well known and need not be enumerated. The general tendency to dispersal inevitably leads to more or less isolation, and it seems probable to many that most species have been finally established in this way. In any event, it is evident to those familiar with the geographic or topographic position of species in reference to one another that this kind of isolation is a factor of very great importance in their determination. It does not produce them, but it gives them an opportunity.

There is also recognized what is called biologic isolation, which means that such variations may occur among closely related individuals that, although they may be associated in one habitat, they become incapable of crossing. This may result from a difference in the season for fertilization, in some structure that prevents crossing, or in various other ways. At present, this kind of isolation does not stand out as a factor in the determination of species so distinct and effective as does geographic isolation.

Mendel's law. — It is evident that whether new species arise by the cumulative results of natural selection acting upon small variations, or by the occasional sudden appearance of wide variations, a still more fundamental problem is to explain variation, which is one of the features of heredity. The study of heredity, therefore, which is fundamental to all evolutionary doctrine, is being prosecuted to-day with remarkable vigor. Conspicuous among the recently developed doctrines of heredity is Mendel's law, so called because it was first announced by Gregor Mendel, an Austrian monk. Mendel's publication of fifty years ago fell on sterile ground and passed into oblivion, until it was brought to light

in recent years by scientific plant breeders, DeVries among others. It is impossible to give an adequate account of Mendelism in this connection, for it has become so extensively developed that only the special investigator can follow its ramifications. Some conception of it may be obtained, however, from the simplest possible illustration.

In the study of heredity the use of hybrids enables the investigator to observe more distinctly the characters of each parent as they appear in the progeny. Using a very simple hybrid, Mendel's law may be illustrated as follows, with the help of the accompanying diagram.



Let A and B represent two species of plants that are crossed; then one of the hybrid plants that result may be represented by AB, which indicates a mixture of the characters of the two parents. When AB produces progeny, the hybrid will "split" in the following ratio: one fourth pure A, one fourth pure B, and one half the mixture AB. In the next generation the A and B plants will produce only A and B plants, and so on through successive generations; but the AB plants (hybrids) will produce offspring that split the characters in the same ratio as before, and so on. It is evident that this provides incidentally a test for hybrids, and that in the case of a hybrid there is a splitting and the separation of a certain proportion of the parent plants. It was this test that DeVries applied to his evening primrose, and as it did not "split" in many generations, he was convinced that he was dealing with a pure species.

It can be understood that such simple hybrids as the one used in the illustration do not represent the general situation in nature or under culture; but they serve to illustrate the fundamental feature of Mendel's law, which is that a hybrid in the second generation splits up in some definite ratio. It is not clear that all hybrids behave in this way; that is, some of them may not be Mendelian hybrids; but the law is prevalent enough to be used as the basis of very much scientific plant breeding and of experimental work related to evolution.

Heredity. — A phase of heredity has been presented under Mendel's law, but the general subject should be considered briefly. Heredity

is the most difficult and perhaps the most important problem in biology. It means the transmission from parent to offspring of a similar structure, a transmission that involves fundamental resemblances with differences in detail. The possible machinery of heredity has been observed, but the factors controlling and determining the product are elusive as yet. Little more can be done than to state the problem.

In the simplest plants and animals every cell has the power of reproducing the whole organism. In the more complex plants and animals this power is restricted, being retained only by the reproductive cells. It is evident, therefore, that the reproductive cells possess a very primitive power, a power that the other cells have lost. Reproductive cells are to be thought of not as cells that have acquired some special power, but as cells that have retained a primitive power that once belonged to all cells. All other kinds of cells may reproduce their own kind, but a reproductive cell can reproduce the whole organism.

Reproduction is not simply cell multiplication, but also cell differentiation, and the organization of differentiated cells into organs, and of organs into the complete organism. Reproductive cells have been made to multiply cells under artificial stimulus; but it is this far-reaching directive power that has baffled investigation.

Any theory of heredity must explain not only likeness to the parent, but also variation from the parent and from every other individual, which is individuality. It must explain ancestral likeness, which is often called "atavism"; and also the sudden appearance of new characters, which after all may be very old ones. In short, the mass of observations awaiting explanation by some law of heredity is enormous.

The student of plant morphology is familiar with the general organization of a living cell. He has learned to recognize in the nucleus the probable machinery of heredity; and in the chromosomes the particular nuclear structure whose behavior suggests a definite relation to heredity. The mingling of paternal and maternal chromosomes in the fertilized egg is the beginning of a series of changes that must be followed eventually; but as yet the particular chromosomes are lost to sight, and their fate is followed only by inference or imagination. Later, male and female chromosomes are recognized again, but only to function in reproduction, and their varying influence in determining the structure of the individual remains unknown.

PART II — PHYSIOLOGY

INTRODUCTION

The relation between the form and structure of a plant and its behavior is very intimate and to a large extent reciprocal. Form and structure in general determine behavior, and behavior, especially as it is itself controlled by external agents, to a great degree determines form and structure. It is not possible at present to discover all these reciprocal relations, much less to describe them in terms of physics and chemistry. Nor is the behavior of plants sufficiently known to be explained in these terms.

Morphology, concerned with form and structure, is particularly interested in how each plant comes to be what it is in the short history of its own life (ontogeny), and also seeks to form a conception of how plants have come to be what they are in the long course of their history since they began to develop on the earth (phylogeny). The former topic is clearly open to experimental study and constitutes the field of experimental morphology. But the latter is much less open to experiment; scarcely at all, indeed, except for the determination of the laws of heredity, a field which has been called "experimental evolution." Obviously such experiments, whether in the field or laboratory, cannot be wisely planned or executed without a thorough knowledge of plant physiology.

A wide range of facts is open also to mere observation, because the ordinary changes in climate and soil, some of which are produced by other plants and animals, affect the form and structure of plants. This field is part of that distinguished from physiology proper as Ecology (Part III). Naturally even the most careful observations need to be confirmed or corrected by experiments. Thus this portion of ecology and experimental morphology are mutually related, and both really form a part of physiology in the broadest sense, and depend upon it. Physiology, in its turn, seeking to expound the phenomena of plant life in terms of matter and force, depends upon the data of chemistry and

physics. In certain directions present knowledge is almost or quite sufficient to permit the framing of physical and chemical explanations. In others the data of chemistry and physics are not yet adequate for this; and in still others it seems now quite improbable that the phenomena can ever be analyzed in terms of matter and force. It must not be forgotten, however, that this is the direction of all recent advances, and that what is hopelessly obscure often becomes beautifully clear as some new vantage point widens the view.

In its broadest sense, then, plant physiology includes the study of the behavior of plants of all sorts, and of all the ways in which this is affected by external agents of every sort. On the one hand it overlaps morphology, and on the other it includes a large part of ecology. In this book, however, it is restricted in the main to a consideration of the behavior of the larger plants, especially seed plants, though in certain cases reference is made to others. In this part no section on reproduction will be found. That topic is relegated to Morphology (Part I), since the purely physiological processes are relatively simple, so far as known, and very much alike, whereas the reproductive organs are very different in different groups of plants and are most significant for their morphology. For convenience, also, the effect of external agents on plants is treated so as to develop and illustrate general principles, whereas the more extended account of specific cases will be found in Part III, on Ecology.

CHAPTER I — THE MATERIAL INCOME OF PLANTS

1. THE PLANT CELL

An organ. — At a glance one sees that the body of an ordinary green plant, such as a bean, is segmented, certain parts being clearly marked off by form from others. The colorless root grows in the soil; the green shoot grows in the air and consists of a distinct stem with lateral outgrowths, the leaves. Anatomically, these parts are *members;* but as the work of the plant is distributed among them, each has its *functions*, and physiologically each is an *organ*.

A cell. — When one of the organs of the bean, such as a leaf, is inspected, one sees that it, too, is made up of parts, the petiole and the leaflets. The latter are composed of ribs and veins, with green tissue, or mesophyll, between. These parts also have certain functions and hence may be called organs. A microscopic examination of the mesophyll reveals that it is composed of minute bits of material which has come to be known as living, and is called protoplasm. Each, individualized, is a *protoplast*, separated more or less completely from its neighbors by membranes which it and they have formed. The membrane and protoplast constitute a *cell* (fig. 619).

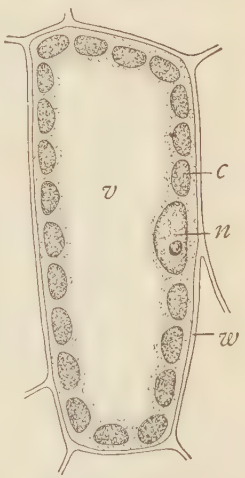


FIG. 619. — Diagram of a mesophyll cell of a leaf; *c*, chloroplast; *n*, nucleus; *v*, vacuole; *w*, cell wall.

Organs of a cell. — When the protoplast is examined more closely, a general translucent material, the cytoplasm, may be distinguished from various inclusions. There are (*a*) many very minute particles, whose nature is obscure, which tend to make the cytoplasm opaque; (*b*) minute clear spaces, more fluid and sometimes watery, the vacuoles, many of which coalesce as they enlarge with age, and form a few relatively very large water spaces or only one; (*c*) a roundish nucleus; (*d*) numer-

ous oval green bodies, the chloroplasts. Of these, the nucleus and chloroplasts, having definite though only partly known functions, are often called organs of the cell.

The unit of function. — The word "organ," then, is applied to parts most diverse as to size and complexity; it designates merely a part when its work is thought of rather than its structure. Since the various parts of a cell do not work properly when separated, the cell may be considered as the unit of function, as it is, for convenience, known as the unit of structure.

Naturally cells accustomed to association with others do not work properly when separated; but there are plants whose whole body is a single cell. This fact has influenced the conception of the cell as a unit.

Work of the protoplast. — What a plant or any part of a plant can do depends primarily upon the protoplasts, since they alone are composed of living substance; but not all protoplasts have the same organs. For example, the protoplasts of the leaf mesophyll, furnished with chloroplasts, can make certain food when properly lighted and supplied with carbon dioxid. But in the higher plants protoplasts which lack these organs cannot form food of this kind under any conditions. The protoplasts of a tuber, having organs known as amyloplasts (starch-formers), are able from suitable material to organize the large starch grains that constitute a form of reserve food of much importance. These grains are not produced except by such special organs.

The cell wall. — Each protoplast jackets itself with a membrane, which usually shuts it off completely from the outer world and from its neighbors, except for some exceedingly minute threads of cytoplasm by which it remains connected with them. These threads, traversing the cell wall, persist from the time of its formation. The protoplasts are much hampered by these walls in certain ways, though compensating advantages doubtless accrue. For instance, the movement of the protoplast is restricted, and it cannot engulf food particles, but is limited to the substances which can dissolve in water and so migrate through the wall. Thus the cell wall becomes a factor of prime importance to the plant.

The cell wall is the most easily observed and striking part of the cell; in fact the word itself commemorates the discovery of the empty chambers of cork and charred wood which Hooke and Malpighi and Grew saw (1667–1671) with their primitive microscopes, and thought the fundamental feature of plant structure.

Removal and alteration of the wall. — The cell wall, formed by the protoplast, is subject to partial or complete removal by it. In green plants it is usually composed at first of cellulose; but pectic substances early appear in it, and with increasing age it is subject to various modifications, which alter its relation to water and thus profoundly affect the conditions of life of the protoplast within.

One alteration to which the wall is subject is known as cutinization, because cutin is deposited or formed within it. Sometimes, as on the outer face of superficial cells, this takes place to such an extent as to form the cuticle, a layer which may be loosened and removed entire from the rest of the wall. Parts of the outer wall adjacent to the cuticle may also become impregnated with cutin to varying degrees. The cuticle and these cutinized layers repel water, so that a minimum only is found in the wall and little can pass through.

By another modification portions of the wall may become gelatinous. When wetted, they take up great quantities of water (sometimes as much as 98 per cent of their wet weight) and swell so enormously as to lose altogether their usual firmness.

Again, the wall may become lignified, a condition characteristic of the walls of woody tissues, whence the name. Lignified walls do not swell so remarkably as gelatinized ones, but they allow water to pass through them with comparatively little resistance.

Water of the plant. — From what has been said it is evident that water forms an important part of the cell; but it is necessary to comprehend its intimate relations to every part in order to understand its full significance. In ordinary land plants water constitutes always over one half and usually about three fourths of their weight. Of the least watery parts, such as wood, it forms one half, and of the most watery parts, such as the pulp of juicy fruits, as much as 95 per cent. In ordinary speech it is common to indicate the general character of an object by naming its most abundant component; as, a wooden table, a brick wall, wood and brick being respectively the dominant but not the only material in the structure. If the water of the plant were visible to the eye, distinct from the other constituent materials, on the same principle a plant might be spoken of justly as water, held in form by other substances mingled with it. This is quite the reverse of the ordinary conception, but its essential truth becomes evident when we consider not merely the quantity of water relative to other constituents, but attempt to picture the relations of water to the various parts of the cell.

Imbibition. — When a plant is placed in dry air, water evaporates from it and its various parts shrink and shrivel. A little shrinkage occurs when plants wilt on a hot, dry day. When water again enters in sufficient quantity, they swell and regain their fresh look. The water may even be driven out entirely from some plants, as certain mosses, and when again wetted, the parts swell and regain partly or wholly their original dimensions. The most obvious of these changes are due to the collapse or expansion of the cells; but that they are not limited to alterations in the dimensions of the cells may be shown by measuring a dry bit of cell wall or a dry starch grain under the microscope, and after wetting, remeasuring it. On examination it appears that almost every substance in the plant body is capable of imbibing water, and of swelling or shrinking as the proportion of imbibed water increases or diminishes. The smaller the quantity of water the more difficult, and the larger the amount the more easy it is to remove it. From the fully swollen gelatinous body of a sea weed, *Laminaria*, some water may be extracted by the pressure of the fingers, while the greatest pressure does not suffice to squeeze it all out, and even by heating it is most difficult to remove the last traces of water.

Theoretical structures of organized bodies. — A study of the phenomena of swelling by imbibition, and of the way in which cell walls and starch grains affect polarized light, permits some inferences either as to the form and position of the particles, or as to the existence of strain or tension between them, by which they are slightly deformed or displaced. These inferences lead to theories of the invisible structure of the cell parts. The particles of which wall and protoplast are composed, it seems probable, are surrounded by water. Whether these particles are the chemist's molecules, linked together in a tense network, or aggregates of molecules (micellae) having a crystalline form, which are features of the two prominent theories, is of only remote significance. In either case the water between them may increase or diminish in amount; correspondingly, the particles approach or recede from one another. When any water is present, it forms a connected whole, however irregular its distribution may be. The particles of the swollen stuff also cohere, and remain so related to one another that when the water is all removed, they regain the form they had before it entered.

Swelling and solution. — In the recovery of the original form is a practical but only a partial difference between the behavior of merely swollen and of dissolved substances. In both cases water wanders in

among the particles and separates them more or less widely. But there comes a limit to the swelling, and no more water enters. If it is removed, the body regains its form and the particles, presumably, their identical position. In solution there is no limit to separation, except by the amount of water present; and when it is removed, the particles rearrange themselves in forms which may be similar to those of the original body, but are obviously not identical with them. Yet swelling may become excessive, as when starch grains are put into hot water or alkalies, and after certain limits are passed the swollen grain will not regain its normal form. By such transitions imbibition merges almost insensibly into solution.

Relations of inner and outer water. — For further understanding it is useful to attempt to picture the relations of the water to the other components of a young cell immersed in natural water. The outside water has particles of many sorts scattered through it; for no matter how pure, in nature all water is really a dilute solution of various substances. The water of the cell wall has so many particles of cell-wall stuff scattered through it that nearly half the volume is cellulose; but it is continuous with the water outside. The water of the cytoplasm and of its inclusions is freer of these substances, *i.e.* it is more nearly pure, because the cytoplasmic particles form only about one fifth of the whole mass. This water, too, is continuous with the water of the cell wall, and with that of the solution outside. The water of the vacuole is still less encumbered with other particles, only one or two per cent, perhaps, but these are of diverse kinds, for the cell sap is a solution of many things. The water here is likewise continuous with that outside through the cytoplasm and wall (fig. 620).

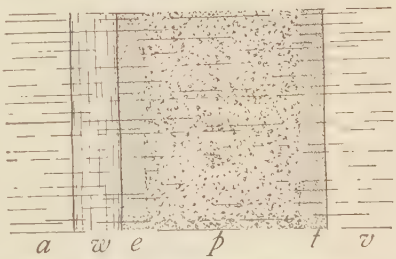


FIG. 620. – Diagram of an imaginary section through the cell wall and protoplast to show the possible relations of water to the cell; *a*, outer water; *w*, cell wall; *e*, ectoplast; *p*, general cytoplasm; *t*, tonoplast; *v*, vacuole (inner water); *e*, *p*, *t*, belong to the protoplast.

Continuity of water. — The picture sketched above may be applied to any plant cell by modifying it to fit special features, and may furnish a working hypothesis, crude though it be, of the invisible structure of organic bodies in general. This hypothesis is conceived to coordinate

the observed facts of structure and of the migration of substances into the plant. The continuous cell wall determines that only substances soluble in water can enter the body. But according to this picture a continuous waterway is provided along which water-soluble substances may travel. Now in order to conceive how this migration occurs, one must have a mental picture of the behavior of watery solutions. To get such a picture it is necessary to bring to mind certain ideas of physicists regarding matter in its various states.

2. DIFFUSION AND OSMOSIS

For convenience, matter is said to exist in three states: gaseous, liquid, and solid.

Gases. — One characteristic of gases is that their particles tend to separate and to occupy to its utmost limits any receptacle in which the gas is placed. If unconfined by impermeable walls on one side, they form no free surface, but show unlimited capacity for diffusion, and their particles may become so dispersed among the other gases constituting our atmosphere as to be unrecognizable by any means at our disposal. This distribution of the particles is independent of any mixing by mass movements, such as those which show as currents or arise by jarring or stirring. On the contrary, it is assumed to be due to the energy of the gas molecules themselves, being hastened by any means which imparts energy, as by the application of heat.

Liquids. — The molecules of liquids are much less mobile than those of gases. When placed in a container, they shape themselves to it and form a free surface that is horizontal under the action of gravity, from which particles may fly off as vapor into the air. In volatile liquids this takes place at ordinary temperatures to such an extent that the process is easily measurable; in others, called non-volatile, the movement is too slight to be observed, or is masked by other changes. Increasing the molecular energy of the liquid, as by heating it (unless it dissociates too rapidly), hastens its conversion into vapor, which behaves nearly or quite as a gas.

Solids. — The particles of solids are still less mobile than those of liquids, so that solids retain more or less perfectly their own shape, except under stress. Some solids, like ice and iron, can be liquefied and then vaporized; others, like camphor, may vaporize without passing through the liquid state.

Solution. — In every state of matter there exists a tendency of the particles to separate, hampered more or less by their cohesion or mutual attraction. Even very dense solids, such as lead and gold, when placed in contact, show intermingling along the line of contact, though this is so slow as to be actually measurable only after a long time.[1] But when certain solids and liquids are brought together, the intermingling occurs so speedily as to attract attention, and the solid is said to dissolve in the liquid. The liquid then is known as the *solvent*, and the former solid as the *solute*. Gases also dissolve in liquids. In like manner when two liquids can be mixed (*i.e.* are *miscible*), their particles become intermingled; then one may be considered as the solvent and the other as the solute; *e.g.* glycerin and water. All gases are miscible and in all proportions; but not all liquids (*e.g.* oil and water), nor all solids and liquids. Otherwise stated, when one substance dissolves another, the two do not always mix in all proportions; usually there is a limit to the ratio of solvent to solute, and when the limit of intermingling is reached (a condition called saturation), any excess of the solute remains undissolved.

Nature of solution. — It is not necessary to the idea of a solution that the mixture should be liquid, though this is the popular usage. A solid, a liquid, or a gas may "dissolve" in a solid and the solution be a solid. So a gas may "dissolve" in a gas and the solution be gaseous. For our purposes, then, a solution is a mixture of substances so intimate that they cannot be mechanically separated; as, for example, by filtration.

The actual chemical state of the substances is not certainly known. Moreover, by mingling finely divided but insoluble substances, such as lamp black, with a solution, many particles of the solute may be taken out, probably by adhesion, so that this sort of partial mechanical separation is possible.

Water as a solvent. — Almost the only liquid which is of much significance in plant life as a solvent is water, and this is capable of dissolving more different substances than any other known; whence it is said to be the most general solvent in nature. In water solutions the particles of the solute behave as those of a gas; they may diffuse to the limits of the solvent, for its boundary forms the only limit to their movements.

Natural solutes. — Water is widely distributed in nature, and comes in contact with many things; first, as it falls in a spray through the

[1] In an experiment in which a rod of lead and a disk of gold were kept in contact for four years, the gold had diffused over 7 millimeters from the contact surface, in amounts appreciable by assaying.

atmosphere, and then as it percolates through the soil and rocks or flows over their surface. Hence, natural waters hold many solutes, and are almost always in position to acquire more if any are removed by chemical action. Thus, the water in arable soils contains everywhere much the same amounts and kinds of mineral salts; for, though soils differ greatly in the proportion of their constituents, the quantities are kept nearly constant by the steady dissociation of the dissolved minerals, by the further solution of any substance which has disappeared from the water for any reason, and by the movement of solutes from one point to another.

Diffusion. — If solutes are free to diffuse through the water to its utmost limits, what determines the direction and rate of this movement? Imagine a crystal of a soluble salt placed in a tumbler of water (fig. 621). The particles fly off from the surface and become numerous in the water immediately adjacent. Here, freed partly from the mutual constraint of the crystalline condition, they may be conceived to be in rapid movement to and fro, colliding often with their fellows where these are most numerous and less often where they are fewer. Hence, in regions towards the crystal, rebuffs are most frequent; consequently the particles are continually working out into parts of the solvent more and more remote from the crystal and the crowd of salt particles, the final result being an equal distribution throughout the solvent. The movement is from the region where the particles are most numerous to that where they are less numerous, *i.e.* from the regions of higher *concentration* of the solute to regions of lower. Or, since gas pressure is conceived to be due to the impact of the molecules on the sides of the container, and since the solute behaves as a gas, it is from regions of higher to regions of lower *pressure.* For convenience, the tendency of solutes to diffuse may be called diffusion pressure or diffusion tension.

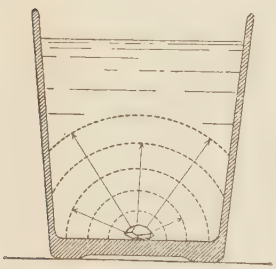


FIG. 621. – Imaginary section of a tumbler of water with a soluble crystal, showing by arrows the direction of diffusion, and by dotted circles the lines of equal concentration.

Rate of diffusion. — The rate of movement of diffusing particles of any solute depends on the *difference* in concentration, or the *gradient* of the pressure. Thus, when a very soluble crystal is put into a solvent, the rate of diffusion is at first rapid, because an infinitely high concentration

of solution is adjoined by a zero concentration; the gradient is "steep" because the solute at infinite pressure adjoins the pure solvent of zero pressure. But the rate constantly falls as diffusion progresses, since the difference at any two points is becoming less and less. The rate is also greatly influenced by temperature, an increase accelerating and a decrease retarding the rate, exactly as in gases.[1]

Osmosis. — Returning now to the conception of the relation of water to the plant cell: it might seem that, given waterways in cell wall and protoplast, any solute, inside the plant or out, might diffuse in any direction in which its concentration is lower. And this would be the case were there no relation existing between the solutes and the material of the separating membranes, the cell wall and protoplasm. These modify the free diffusion; diffusion through membranes or partitions is distinguished as *osmosis*, and the pressure which solutes may exert on the container is known as osmotic pressure.

Unlike gas pressure, to which it is comparable, osmotic pressure cannot be measured directly except with great difficulty. It is calculable from the amount by which a solute lowers the freezing point and raises the boiling point of the solvent.

Permeable and impermeable membranes. — Suppose in a closed glass vessel (fig. 622) a glass partition divide *A*, pure water, from *B*, a watery solution of salt. No interchange of water or salt between *A* and *B* is possible through such a partition, whence it is said to be impermeable. But if the partition be made of some substance with whose particles salt particles can mingle — a substance, that is, with which salt forms a solid or semi-solid solution — then the salt particles which by diffusion reach the *A* side of the partition may fly off thence into the water, *a*; and they will do so, provided the attraction of the water for the salt is greater than that of the partition stuff for the salt. The nature of the partition, then, determines whether any substance may pass through it, and of course modifies the rate of its diffusion.

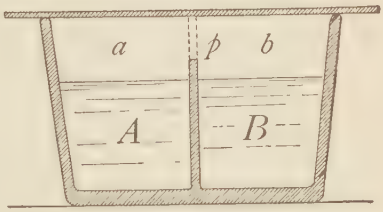


FIG. 622. — Diagram: *A*, pure water; *B*, watery solution of salt, or sulfuric acid; *p*, portion of the partition supposed to be removable; *a*, *b*, air.

[1] To avoid misunderstanding it may be necessary to add that under like conditions each solute diffuses at a rate peculiar to itself.

This is well illustrated by using air as the partition. In fig. 622, suppose *A* to be pure water and *B* sulfuric acid, with the impermeable glass partition reaching only a little beyond the top of the two liquids, the space above them being filled with air. Water (as vapor) can mingle with air, *a;* sulfuric acid does not vaporize measurably; *i.e.* the air, *b*, is practically impermeable to it but permeable to water. Water particles therefore reach the *b* surface of the air partition and enter the sulfuric acid. Hence the water level in *A* falls; the acid level in *B* rises.

Or, again: if one place carefully in a tumbler (fig. 623) chloroform, *c*, water, *w*, and ether, *e*, the water may be considered as the partition. Ether, being freely soluble in water, diffuses into it and reaches the surface of *c*. Being also soluble in chloroform, it moves on from this surface, diffusing in the chloroform. The chloroform, being only slightly soluble in water, diffuses into it but slightly. Finally, there remain only two mixtures: the water saturated with ether and chloroform, and the chloroform saturated with water and containing the rest of the ether. This experiment illustrates not only the solvent action of the partition, but also the way in which the relations of solubility between the partition and the liquids that it separates determine the dominant direction of diffusion.

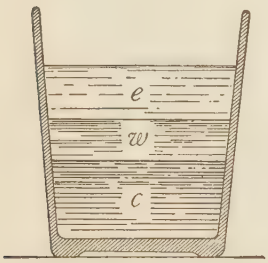


FIG. 623. — Diagram: *c*, chloroform; *w*, water; *e*, ether.

The cell wall membrane. — Among the plant membranes through which solutes pass, the cell wall seems to exercise little selective influence. It is permeable to most if not all substances presented to it in nature. For, externally, these are chiefly mineral salts; and internally, the cytoplasmic membranes exclude from contact with it any substances that it also might not allow to pass.

Cytoplasmic membranes. — The protoplast behaves quite differently from the cell wall. It is obvious from microscopic examination that it is not uniform in structure. There is always next to the cell wall a delicate cytoplasmic layer, the ectoplast, and each vacuole is bordered by a similar layer, a tonoplast (fig. 620).

Since a layer, apparently of the same sort, is formed at the surface of a fragment of protoplasm released by violence from the cell wall, it seems probable that these layers are the result of a change wrought in the physical structure of the cytoplasm by contact with solutions of a certain sort, rather than that they are permanent organs, as they were once held to be. They are perhaps advantageous in protecting the cytoplasm from further change.

However formed, they are limiting membranes not only in the sense of bounding the protoplast, but also in the sense of admitting and emitting some only of the great variety of solutes that come into contact with

them. Yet the share of the rest of the protoplast in this discrimination is not to be overlooked; and since it is impossible to analyze the action of each part, we may for convenience consider the protoplast as *a* membrane between the vacuole and the outer world. But for substances in the protoplast itself the ectoplast may act alone.

Selective action. — The chemical composition of the cytoplasm being almost wholly unknown and doubtless variable, no clear statement can be made as to the mode of its discriminative action. It is known only that it allows many substances to pass through readily and debars others; and further, that some substances, which are usually denied passage, are permitted to pass under other conditions. These relations are best explained by the theory that solubility in the membranes is prerequisite to osmosis. If so, a change in composition of the cytoplasm might account for the change in permeability that is observed on occasion.

It is quite possible that local differences in the composition of the cytoplasmic membranes (a sort of mosaic composition) may permit the passage of different substances at different places.

Variable selection. — The welfare of the organism is largely dependent on the discriminative action of the cytoplasmic membranes, for substances requisite to food-making are allowed to enter; and foods are not permitted to diffuse out and be lost. Chemical transformations of the most varied kind occur within the plant, both among the substances that enter it and are elaborated into foods, and also among the foods that are assimilated. Of course each change in chemical nature changes the relations of the substance to the protoplast and may modify thereby its diffusibility through it. Moreover, without known chemical change, the mere presence of one solute may greatly modify the behavior of another, either by changing the membranes, or by its direct influence upon the other solute. With membranes capable of change, and solutes capable of change, and the almost unknown extent of the influence of one solute on another, the complexity of the phenomena of osmosis has almost baffled investigation hitherto, but some hopeful progress has been made recently in the discovery of factors determining the permeability of protoplasm.

It cannot be too strongly emphasized that the "selection" above described has in it no element of choice, nor does it depend upon the "needs" of the plant. On the contrary, it is purely physical, and depends solely upon the mutual relations of the substances (membranes and solutes) which the conditions bring into contact.

3. TURGOR AND ITS CONSEQUENCES

Immigration of water. — The fact that there are formed within the cells certain substances to which the cytoplasmic membranes are nearly impermeable, and that they may accumulate to a considerable extent, insures the entrance of water into such cells either directly from the outside or indirectly from adjacent cells in which the solutions are less concentrated. The mode of this movement may be conceived thus. It is known that the presence of any solute reduces the vapor pressure of water; which, in terms of current theory, means that there are fewer molecules of water per unit volume over a solution than over pure water under the same conditions. Thus in fig. 622, p. 305, if *A* be pure solvent and *B* the watery solution, the actual pressure of water vapor in *b* will be less than in *a*. If the partition between *a* and *b* be removed, the difference in pressure would cause more particles of water vapor to move into *b* in a unit of time than would diffuse in the reverse direction. If the whole partition were permeable to water and not to the solute, the same movement would take place through the partition; this occurs, it may be conceived, because the presence of the solute particles reduces the internal pressure of the water, whose particles thus diffuse, in the common fashion, from regions of higher to regions of lower pressure. The conditions determining the movement of the water are created, be it noted, by the number and nature of the solute particles.

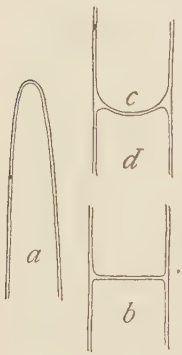


FIG. 624. — The cell walls of a *Cladophora*: *a*, a young tip of a filament; *b*, a division wall in the middle of a filament; *c*, a division wall next to a dead cell (*d*).

Turgidity. — As a consequence of the migration of water into the vacuole, the protoplast is forced outward against the cell wall, which, being elastic, is stretched thereby, unless the pressure is balanced by an equal pressure from an adjoining cell. Superficial cells, without exception when healthy, have the free wall convex outward. The filamentous algae have the free end often very convex (fig. 624, *a*), but the partitions between cells at a little distance from the end are practically plane (fig. 624, *b*). If the filament be broken or a cell dies, the adjacent walls, previously plane, at once bulge out (fig. 624, *c*) on account of this internal pressure. When a cell is surrounded on all sides by those of equal internal pressure, its walls are plane.

The condition of cell walls in a massive tissue may be comprehended clearly by inspecting a mass of bubbles such as may be formed by blowing air through a tube into a soap solution.[1] The outer bubbles will have a convex surface, but plane films divide the air bubbles in the interior. Pricking a superficial bubble gives opportunity for the plane walls of those adjacent to it to bulge, because the internal pressure is now unbalanced.

A cell thus overfilled with water, with the elastic wall stretched, or under strain and ready to stretch, is said to be *turgid*, and the condition is designated as *turgidity*. Manifestly, turgidity depends upon two factors: the presence of a solute or solutes in sufficient amounts, and an adequate supply of water.

Turgor and osmotic pressure. — The pressure developed within the cells, when an adequate amount of water is at hand, may equal the osmotic pressure of the solutes to which the cytoplasm is impermeable. Obviously, the osmotic pressure exists, whether or not it exhibits itself; it exhibits itself by stretching the elastic container only when sufficient water can enter; this particular exhibition of it is known as *turgor*,[2] or turgor pressure. Thus within the cell there exists both osmotic pressure and turgor pressure; the latter is a sort of hydrostatic pressure dependent upon the former for its existence and probably upon the resistance of the protoplast and the cell wall to filtration for its amount. It is seldom likely, therefore, to equal the osmotic pressure.

Thus, in the cells of the sugar beet, the cane sugar alone has an osmotic pressure of 10 or 11 atmospheres; and there are certainly many other solutes which would add greatly to this. But the turgor pressure can only reach a point at which water will filter through the cytoplasm and cell wall, and this is probably less than half the osmotic pressure of the sugar alone.[3]

That the osmotic pressure is always ready to produce turgor is shown by the fact that flaccid cells placed in pure water quickly become turgid.

Plasmolysis. — If a turgid cell is placed in a solution more concentrated than that within it, water emigrates from the cell, which then becomes more or less flaccid. By measuring turgid cells, or making careful

[1] This may be made of a plain glycerin soap. More durable bubbles may be made from this solution: Shaved white Castile soap 10 gm. by weight; warm water 400 cc.; dissolve. To 15 parts by volume, add glycerin 11 parts. This will be improved by allowing it to stand for a week, cooling over night to 3° C. and filtering cold until limpid.

[2] The term is not always thus restricted; it is often used as synonymous with turgidity.

[3] Further studies of this subject are much needed, especially as the usual mode of testing osmotic pressure by plasmolysis has been shown to be faulty.

camera drawings of them, comparison after treatment with an appropriate solution shows the shrinkage of the wall to its unstretched size. If the outside solution remains more concentrated after a loss of water from the cell just sufficient to permit the return of the wall to its unstretched condition, water continues to leave the cell. As a consequence of the diminished volume of cell sap in the vacuole the protoplast is dragged away from the wall, if this is rigid enough (as it often is) to support itself; or if not, the whole cell, wall and all, is collapsed. Usually only extreme shrinkage from loss of water, resulting in separation of protoplast from wall, is called plasmolysis; but obviously, plasmolysis has two phases, inseparable except arbitrarily. It begins with the first emigration of water, and up to the complete recovery of the cell from previous stretching, it can be detected best by measurement. In its second phase the further emigration of water is made evident by the more or less extensive collapse of the protoplast.

Rigidity from turgor. — The emigration of water which takes place when a turgid cell is surrounded by a more concentrated solution is only one way by which turgor is reduced or plasmolysis produced. The evaporation of water may produce the same effects. When a flexible organ, like a leaf or a young shoot, loses water to such an extent that its cells are no longer turgid, the parts bend by their own weight; the edges of the leaf and the tip of the shoot droop. To the touch they are less rigid than before. This observation shows one effect of turgor. Thin-walled cells in masses, such as form the greater part of young shoots, leaves, and young roots, are rendered much more rigid by the strains set up in the mass by turgor. Turgor tensions in the smaller and in the less differentiated plants, as well as in the younger parts of all plants, are thus important in maintaining bodily form; whereas in the older parts, especially of large plants, mechanical tissues, characterized by thickened and altered cell walls, provide the requisite rigidity.

Growth and turgor. — Besides its rôle in maintaining bodily form, turgor has important relations to the growth of cells, especially in the phase when enlargement is the marked feature (see p. 420). At this time water is entering in relatively large amount, and turgidity is prerequisite to the permanent enlargement. The cells of flaccid tissues do not grow larger. Whether stretching is merely a mechanical necessity for such growth, or whether growth is dependent upon the increase in solutes, which would likewise determine the increase in turgor, or whether both conditions are necessary, is not certainly known.

Sap pressure and turgor. —Turgor plays an important part also in "root pressure" (see p. 336), by reason of which, under certain conditions, water is forced by the cells of the cortex into the conducting tissues, whence it may escape by filtering through the walls, or directly if these are cut or broken. Further, it is probable that turgor is indispensable for the excretion of water and various solutes from superficial cells. But this may be treated better in connection with the topic secretion (p. 337).

4. THE PERMEABLE REGIONS OF ROOT AND SHOOT

Plants and water. —Most if not all of the simpler algae and fungi, many of the liverworts and mosses, practically all submersed plants, and the young stages of even higher land plants are readily permeable to water and to various solutes in every part of the body. In such case they must grow in water or in very damp places. For, if water may be readily admitted over the whole surface, it may be almost as readily lost from the whole surface; it will evaporate whenever the air in contact with any part of the surface is not saturated with water vapor, and this is the usual condition.

Terrestrial plants. —The earliest plants on the earth's surface, it is likely, were aquatic; and in the course of time plants developed that were adapted to temporary exposure on the shore rocks or along the beaches, then to longer exposure and drier ground, until the land finally was occupied by plants which are so constructed that they can expose a large part of the body continually to moist though unsaturated air. The deserts even, with only a meager rainfall, are by no means barren of vegetation, but support hosts of plants, which are able to secure the scanty moisture from the soil and to avoid in the growing season excessive evaporation into the very dry and often very hot air to which they are exposed. The prime requisite to terrestrial life is some means of reducing the evaporation from aerial parts to an amount which can be replaced by the water entering those parts of the body that remain in contact with it.

The root system. —The members of the higher plants constantly in contact with water pertain chiefly to the root system.[1] Of the root sys-

[1] In some plants the underground stems and leaves (scales) are also in contact with water, but they are almost impermeable to it, and hence may be neglected in this connection.

tem, however, only the younger parts are permeable to water, since with age the surface cells become altered, or usually are underlaid and finally replaced by corky or cutinized tissues, whose walls are nearly waterproof. But as the roots are growing at the tips and branching, there are always young and permeable parts.

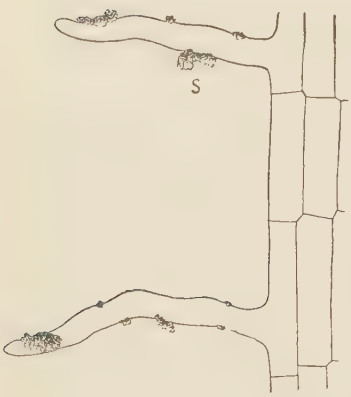


FIG. 625. — Root hairs of lettuce, with adherent soil grains (*s*). — From PART III.

Root hairs. — The surface cells of the young root in most land plants, at a short distance behind the growing apex, branch, sending out tubular extensions, the root hairs (fig. 625), which push their way among the soil particles, displacing some and being deformed by crowding against others, to which they often adhere strongly. These root hairs increase 5–12-fold the permeable area of the root, and by their size and radial position come into immediate contact with a cylinder of soil 3–8 mm. in diameter (fig. 626). They anchor the young root thoroughly, since they adhere so firmly to the soil particles that they tear away from the root when that is pulled out of even the loosest soil; and if by chance they come away, they bring with them the adherent grains. The root hairs are transient, not living through even one growing season. They die away on the older parts of the roots, from which the hair-bearing cells usually slough off; but new hairs are being formed continually, during the growth of the root in length, just behind the advancing apex. (See Part III, p. 495, for variation of root hairs and for kindred topics.)

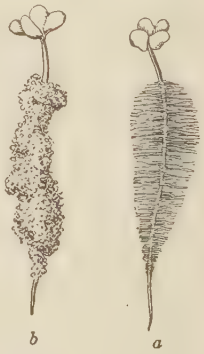


FIG. 626. — Seedling of mustard; *a*, grown in moist air; *b*, grown in sand and withdrawn to show mass of soil grains clinging to root hairs. — After SACHS.

Soil. — The soil, into which roots clothed with root hairs spread, consists of particles of weathered or comminuted rock of various kinds, usually

mixed, especially in the upper part, with more or less organic matter, the offal of antecedent animal and plant life. The soil particles are of various sizes and kinds, and the soil is often named accordingly. Thus there are gravelly, sandy, clayey, and humus soils according to the amount of gravel, sand, clay, or humus present. An indefinite variety of mixtures also occurs, as in loam, with appropriate descriptive names. The texture of the soil depends chiefly upon the size of the individual particles; but when very fine, and especially when repeatedly wetted and dried, these often become aggregated into compound grains, as is obvious in clay. The sort of rock from which the soil was made, the size of the particles, their state of aggregation, and the proportion and character of organic matter, determine the relation of water to the soil, and so the freedom and extent of its movement.

Soil water. — Of the water which falls upon the surface as rain all may percolate into the soil, or part may run off. The character of the soil and of the vegetation on the surface, the slope, the rate of precipitation, and the existent water content, determine the fate of the falling water. A loose dry soil of level surface, a soil cover of leaves or grass, and a gentle rainfall, tend to reduce the run-off to a minimum. The water which percolates into the soil enters the spaces between the soil particles, which it fills more or less, driving out the air and adhering in the form of films to the component particles, when it does not fill the spaces completely. The thicker the films, the less firmly the molecules more distant from the surface of the soil particles are held; so that gravity suffices to carry down to lower and lower levels a certain amount of the percolating water. This may drain away as subterranean streams or may remain, saturating the soil at a certain level and forming thus the "water table," approximately parallel to the surface and at a variable distance from it.

Capacity of soils for water. — When all the water that will sink to the water table in a well-drained soil has drained out of the upper regions, an amount varying according to the physical characters of the soil remains, adhering to the grains. The smaller spaces are still filled; the larger contain bubbles of air which have come in from above as the water sank. If the soil particles be very small and close together, a greater quantity of water will be held than in a loose, coarser soil.

This seems anomalous, but as the amount of water adhering to the surfaces will be almost proportional to the surfaces themselves, it may easily be comprehended by calculating the area of 1000 spheres each 1 mm. in diameter, which could

be packed into a cubic centimeter, in contrast with the area of 1,000,000 spheres each 0.1 mm. in diameter occupying the same place. In the first case the area would be 3141.6 sq. mm.; in the second, ten times as much, or 31,416 sq. mm.

In coarse soils, therefore, such as sand, water largely drains away; whereas in fine soils, such as clay, it is held, and it may be so firmly held as to preclude the admission of more, once the soil is saturated; whence a layer of clay often forms a "hard-pan," in which water collects as in a basin, or over which it runs. Humus soils hold much water, because the particles of organic matter, besides being covered by the usual films, are not only porous, thus admitting water to the interior spaces, but are also able to imbibe it by their very substance.

Capillary ascent of water. — If equilibrium were momentarily reached among the water films in the soil, it would be upset the moment any water evaporated from the upper grains, for the water film that clothed them would thereby become thinner. This would at once cause a rearrangement of the water in all adjacent films, because the adjacent water particles are pulled more strongly to the places where the film is thin than they are held where it is thick. Thus evaporation from the soil causes, on the whole, an upward movement of the water from the deeper parts of the soil, a disturbance which extends as far as is permitted by the resistance offered by the attraction of the soil particles and by the viscosity of the water. As this effect may reach the water table, the result of evaporation is to lower it; its level rises after heavy rain and falls in prolonged drought. Not all the water which enters the soil can leave it, either by drainage or evaporation. Even if a sample of the soil be placed in the air, very thin films of water remain when it is "air-dry" and seems dry as dust. Only by heating above 100° C. can all moisture be driven off.

Migration of soil water into roots. — When a root penetrates the soil and root hairs develop from all sides, the entire surface becomes clothed with a film of water just as is the case with the soil grains. When some of this water enters a root hair or any part of a surface cell, the water film becomes thinner and there takes place the same sort of readjustment as is produced by evaporation of water at the surface of the soil, with the same general movement of water, in this case toward the root. In both cases even distant parts of the soil may thus furnish water to make good the loss. All such movements of water, being mass movements and not diffusion movements, involve the transfer of any solutes present; whence it comes that solutes from a distance may be brought into the vicinity

of a root and may enter it if the conditions permit. But inasmuch as the mineral solutes in the soil waters are very similar, no matter what the character of the soil may be, this is probably of less importance to the plant than it would seem to be at first sight.

Available water. — By no means all of the water in the soil is free to migrate into the roots. There comes a time, as the films about the soil particles become thinner and thinner, when the adhesion of the water to the soil grains is equal to its diffusion tension. Leading up to that equilibrium, it grows increasingly difficult for the plant to balance its loss of water by that entering; its cell sap has become more and more concentrated; and when the outgo surpasses permanently the income, permanent wilting usually ensues and often more or less extensive death of the foliage.

The water content of a soil from which no more water can enter a plant manifestly depends upon the plants concerned, the nature of the soil, and other physical factors. It is no fixed quantity in any case, and at best can be determined only roughly. To say that it is in sand less than 0.5 per cent, in clay about 10 per cent, in loam about 12 per cent, in humus about 14 per cent, and in muck about 20 per cent, is merely to indicate the order of magnitude, not to state a fixed amount. These figures become more instructive when compared with the total capacity of such soils for water, which runs about as follows: sand, 15 per cent; clay, 50 per cent; loam, 65 per cent; humus, 70 per cent; muck, 120 per cent.

Effect of roots on soil. — A considerable amount of carbon dioxid (CO_2) and less quantities of other substances diffuse from the root into the soil-water films. Solution of carbonates is increased by the presence of CO_2 in water, as is shown by the readiness with which a polished marble plate may be etched by roots traversing its surface and giving off CO_2. Reactions due to other solutes which diffuse from the root, or to excretions from it, may determine the solution of other sorts of soil particles, and the substances so dissolved may then enter the root. It is not known that these changes so produced in the soil are of any considerable importance in plant life. Whether by diffusion from the roots of live plants or by the decomposition of dead roots, or by both, it is certain that various complex organic compounds, not yet fully known, exist in soils, which may interfere seriously with the growing of plants thereon. In certain soils the character and quantity of these little known substances are so injurious that the soils are almost sterile. Even a watery extract from them proves harmful. In such cases the

soil can be improved by mechanical and chemical treatment designed to remove or destroy the harmful compounds. The rotation of crops may find partial explanation herein; the excretions and decomposition products of a given crop may be injurious to the same plants, but less so or not at all to others. Even manuring may prove to have its value less in the compounds put into the soil than in the improvement of soil texture and the destruction of the deleterious compounds in it.

Entry of water. — The cells bearing root hairs and the adjacent ones are so constructed as to facilitate the immigration of water and various solutes. The cell walls are thin and the protoplast apparently forms only a thin sheet over the inner surface, the greater part of the cell being occupied by a huge sap cavity. The cell sap is usually a more concentrated solution than the water outside; the internal pressure of the water is consequently less (p. 308), and water enters, distending the cell until the elastic recoil of the stretched wall is sufficient to balance the osmotic pressure of the solutes, or to exude as much water as enters.

Entry of solutes. — At the same time, if any solutes to which the protoplast is permeable exist in the soil water, but either not at all or in less amount in the cell sap, they will diffuse into the cell. But their movement is as independent of the movement of the water as are the conditions of such movement; *water and solutes move independently.* If any solute which enters thus is not changed or stored in the plant, *i.e.* if it is not removed *as such* from solution, it may attain equilibrium inside and outside the plant, so that no more enters; but if it is removed by being chemically changed or by being stored, more constantly enters.

Entry and exit *via* roots. — The root therefore possesses permeable surface cells always in contact with soil water, through which water and a variety of solutes, chiefly oxygen and mineral salts, make their way, under the conditions already set forth regarding osmosis. At the same time, the root permits through these same surfaces the outgo of any solute formed in the cells, to which the cytoplasm is permeable, that does not exist at equal or greater pressure in the soil water. It is even conceivable that water would pass out thus, were it possible for the soil to become sufficiently dry. Artificially this can be demonstrated; it has not been shown that it occurs in nature. When the roots are exposed to air, as in transplanting, especially if the plants are to be transported far, it is necessary to guard against excessive loss of water by evaporation from the roots; and the quick drying of exposed roots is a most obvious danger in transplanting.

Aerial permeable regions. — Land plants possess also certain permeable regions on the aerial parts of the shoot. Small plants that grow in wet places, where the air is very moist or nearly saturated, might safely have all aerial parts permeable, because evaporation is slow and the distance from root to aerial surface short. Moreover, spray or rain falling on such parts may enter there, as well as soil water by the roots. But larger plants could not exist in ordinary dry air were their permeable aerial surfaces freely exposed; for if accessible to rain, the evaporation would be dangerously great. So far as protection is concerned, large plants with aerial shoots might thrive (1) if they were completely waterproofed, thus checking all evaporation, or (2) if their damp surfaces were shielded by drier partial coverings, thus reducing evaporation and necessarily excluding water.

Waterproofing *vs.* salts. — There seems to be no *a priori* reason related to the necessary supply of water and salts why the first of these alternatives should not have appeared in land plants. Structurally, it would be quite possible to waterproof the aerial parts completely, since plants do check water loss by such means in certain places. In such a case, enough water for other purposes might undoubtedly enter, since enough to supply the great evaporation now enters by the roots alone. But, it is objected, this would have prevented the intake of sufficient salts. As to that, it is not probable that stopping evaporation, and therefore the large inflow of water at the roots, would interfere with the supply of salts. This is rendered probable, because diffusion of solutes is independent of the movement of water; and to assume, as this objection does, that the solutes are carried along by the entering water which replaces that evaporated, contravenes all that is known about osmotic movement. Further, it is supported by the observation that in the rain forests of Ceylon (and doubtless elsewhere) there are regions of luxuriant vegetation where for months at a time the rain ceases only to be replaced by a mist. In such conditions evaporation is almost impossible. It cannot, therefore, be necessary to the adequate supply of solutes from the soil. It is difficult or impossible to create such conditions experimentally; and ordinary plants, accustomed to evaporation, are so upset by being grown in a saturated atmosphere that most culture experiments to ascertain the rôle of evaporation have failed. The few that have resulted in healthy development indicate also that evaporation is not necessary, so far as a supply of salts is concerned.

Waterproofing *vs.* gases. — Though water and salts might still be admitted, a complete waterproofing of aerial surfaces would exclude the gases of the air, because all substances must enter in solution. So, as a matter of fact, plants possess aerial surfaces of large extent, freely permeable, but shielded by covers which, while more or less waterproof, are perforate, so that gases have access to the moist cells underneath. There is one gas, oxygen, needed by almost every plant for respiration, which the terrestrial plants can get satisfactorily only from the atmosphere. There is another gas, carbon dioxid, which is absolutely essential for the food making of green plants, and this likewise can enter land plants only from the air. As the food made by green plants is the sole supply for them and for most other living things, even for man, and further is the chief source of energy for doing the world's work, it is evidently of some importance that the aerial parts of green plants should expose wet surfaces to the air and so make possible the solution and admission of oxygen and carbon dioxid.

Protective tissues. — The admission of oxygen and carbon dioxid by the smaller plants, mosses, liverworts, and the like, is made possible by the fact that the whole surface of the body is moist and therefore permeable. But the larger plants expose wet cell walls only as the bounding surfaces of internal chambers that constitute an aerating system, shielded by a nearly waterproof epidermis or a layer of cork tissue. The outer wall of the epidermis has its outermost layer so completely cutinized as to constitute a continuous sheet, the cuticle; and the subjacent layers are often infiltrated with cutin to a greater or less extent. Besides this, the epidermal cells not infrequently form wax, resin, and similar substances which are secreted in granules or continuous sheets on the outer wall. These substances all repel water, so that only minute amounts occupy these parts of the wall; consequently very little can escape into the air as vapor. On the older parts of the stem, the epidermis is at first underlaid, and later, sloughing off, is replaced by layers of cells, which, before losing their living contents, impregnate the walls with suberin, so that they become nearly impermeable to water (*cork*). Both these superficial waterproof tissues, epidermis and cork, are perforate at numerous points (stomata and lenticels), which communicate with and indeed form a part of the aerating system. (See Part III on cutin and cork.)

Aerating system. — This is a network of canals and spaces, of the utmost irregularity in land plants, and connected throughout. The

passages are formed gradually among the parenchyma cells by partial separation as they enlarge. At first all cells are coherent with their neighbors, a necessity of the mode of division; but unequal growth and turgor produce strains which split the common wall at the corners and sometimes along whole faces (fig. 627). In submersed water plants the aerating system attains its most marked development; huge canals arise in the softer tissues of the stems and leaf-stalks (fig. 628), and in

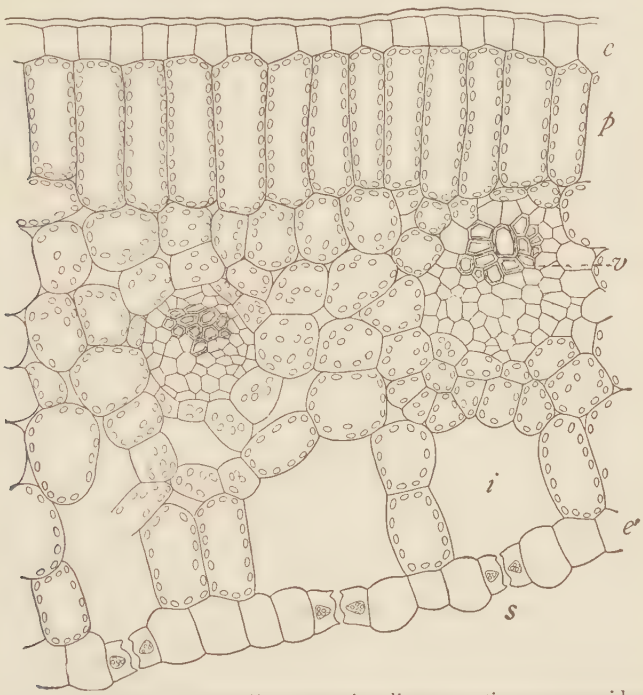


FIG. 627. — Cross section of leaf of lily, somewhat diagrammatic: *e*, upper epidermis; *e'*, lower epidermis, with stomata, *s*, in cross section; *p*, palisade; between *p* and *e'*, spongy tissue, with large intercellular spaces (*i*) below stoma (*s*) and vein (*v*). — From PART I.

other parts branched cells, the branches in contact only by their tips, leaving large space for gases. These inner chambers in submersed aquatics do not communicate with the atmosphere directly; they contain gases which have come out of solution in the adjacent cells and constitute an internal atmosphere into which gases may diffuse or from which gases may migrate into the living cells (of course in solution). **(See further, Part III, p. 551.)**

Stomata. — The aerating system of the terrestrial plants, and of water plants not normally completely submersed, communicates with the atmosphere freely, because certain cells of the epidermis, predetermined by the mode of their development, break apart through the central portion of their last-formed division wall. As immediately beneath them an air space of some size develops, this establishes a passage to the outer air. These two crescentic cells of the epidermis are the lips of a mouth-like slit called a *stoma;* the two lips are called *guard cells* (fig. 629). The guard cells differ from other epidermal cells in their crescentic form and smaller size, and in having chloroplasts which are usually absent from other epidermal cells. Their walls are also peculiarly and unequally thickened (see also Part III, figs. 794–806). Their turgor variations, the unequally thick walls, and their position with respect to the adjacent cells make them change shape, with increasing turgor becoming more arcuate and with lessening turgor straighter. The effect of these changes is to widen or narrow the slit between them, so making more free or restricted the passage of gases either by flow or diffusion.

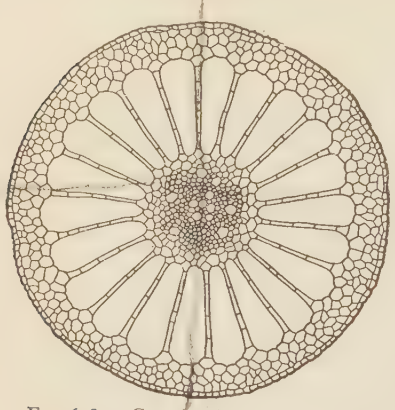


FIG. 628. — Cross section of stem of *Myriophyllum*, with air canals. — From PART III.

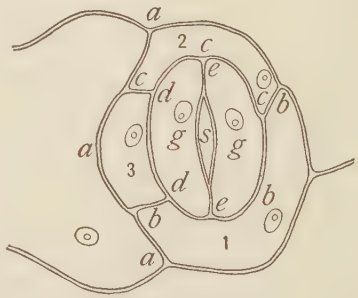


FIG. 629. — Stoma of *Sedum*; *a*, *a*, *a*, first wall, cutting off mother cell of stoma; *b*, *b*, *b*, second; *c*, *c*, *c*, third; *d*, *d*, fourth; *e*, *e*, final wall; the latter, forming the two guard cells, *g*, *g*, partially splits to form the slit (*s*); 1, 2, 3, subsidiary cells.

Size and number of stomata. — A stoma is very minute; the area of the pore when open, in thirty-seven sorts of cultivated plants, averages 0.000092 sq. mm. But their great number on those organs (such as leaves) in which the admission and exit of gases is most free, makes up for their small size. Both features will be grasped better by this statement: in an area equal to that of the dot here printed (●), there are on the under side of the apple leaf over 1400

stomata, and on the under side of the olive leaf about 3700. The following table (after Weiss) shows the numbers per square millimeter in various common plants.

Name of plant	Number of stomata		Name of plant	Number of stomata	
	Upper side	Under side		Upper side	Under side
Olea europaea (olive) . .	0	625	Zea Mays (Indian corn) .	94	158
Castalia odorata (white water lily)	460	0	Betula alba (white birch)	0	237
Helianthus annuus (sunflower)	175	325	Berberis vulgaris (barberry)	0	229
Syringa vulgaris (lilac) .	0	330	Populus deltoides (cottonwood)	89	131
Solanum Dulcamara (bittersweet)	60	263	Pinus Strobus (white pine)	142	0
Pisum sativum (pea) . .	101	216	Avena sativa (oats) . .	48	27
Ficus elastica (rubber plant)	0	145	Lilium bulbiferum (tiger lily)	0	62

So far as plants have been examined, it appears that a large majority of mesophytes have less than 200 stomata to the square millimeter, and a fair average is perhaps 150. (See Part III, p. 556, on variations in the structure and distribution of stomata, and the causes thereof.)

Transpiration. — Since the intercellular spaces are bounded by moist cell walls, freely permeable to water, they are always filled with air which contains more or less water vapor. This vapor diffuses through the stomata into the drier outer air, and being lost from the plant will be replaced in whole or in part by water entering the root. At the same time, since the walls of the epidermal cells contain a little water, some evaporation takes place directly from them. The total evaporation of water under these conditions is designated as *transpiration* (see p. 323).

Exit but no entry for water. — The aerial parts are constantly losing water because they are permeable; at the same time, there is practically no opportunity for the admission of water, even when such parts are deluged by it. Ordinarily rain comes into contact only with a nearly waterproof surface, the cuticle. It cannot easily penetrate the minute stomata, even when they occur on the upper surface of leaves, for there

are usually some special substances or structures that repel water; and so it does not come into contact with the wet and permeable walls of the internal cells. Here then is an arrangement, not found elsewhere in the plant, by which water may leave the body rather freely, yet practically cannot enter it when conditions are reversed.

It may be assumed that there may enter the cuticle, when wet, amounts of water corresponding to those that evaporate from it when dry. The revival of wilted plants after the foliage is sprinkled, however, is due chiefly to checking the evaporation; yet the trifling amount of water entering tends to the same result.

Entry and exit of gases. — The aerial parts facilitate the entry and exit of gases. The external atmosphere communicates freely with the internal atmosphere of the intercellular spaces by way of the stomata. Any oxygen or carbon dioxid in the air of the intercellular spaces may dissolve in the water of the cell walls and then migrate into the adjacent cells, if the pressure of these solutes is less in the cells than in the internal atmosphere. In like manner either may diffuse into the internal atmosphere when the reverse conditions exist. The solubility of CO_2 and O_2 in water under like conditions is very unequal, the former being about 30 times as soluble at ordinary temperatures as the latter. The rate of diffusion is also unequal. The quantity of each used or produced by the plant likewise differs. These factors all play a part in determining the amount of gas which enters or leaves. As the composition of the internal air fluctuates on account of subtraction or addition of CO_2 or O_2, a difference is created between the internal and external atmosphere, which leads at once to diffusion through the stomata in a direction determined by the existing inequality in pressure of either gas.[1] Nitrogen, the only other considerable constituent of air, is neither used nor produced; hence practical equilibrium between the N_2 of the air and the N_2 in solution in the plant is early attained, and this equilibrium is scarcely disturbed thereafter.

In submersed plants the oxygen and carbon dioxid are dissolved in the water and find admission at any permeable surface, like other solutes.

[1] Further discussion of the rôle of these gases will be found in the sections on Photosynthesis (p. 363) and Respiration (p. 403).

CHAPTER II — THE MATERIAL OUTGO OF PLANTS

1. TRANSPIRATION

The term transpiration. — Frequent reference has already been made to the most important outgo of material from the plant body — the water evaporated from the aerial parts. This was long ago called *transpiration*, after the analogy of the exhalation of water vapor from the lungs, with whose movements, however, it has nothing in common. It is considered by many to be a function of the aerial parts, something which they actively *do*, in which case a special name would be quite appropriate. It is better, however, to look upon it as a process in which they are passive. In this case evaporation is no more a "function" of a wet leaf than it is of a wet towel, and the need of a special term is less evident. Yet the word is convenient as a short form for the expression, the evaporation of water from live plants.

Evaporation. — When a dish of water is exposed to air which contains less water vapor than it can hold, more water particles will fly off into the air in a given time than will fall into the water from the air; hence the volume of liquid will be diminished; the water evaporates. The rate of evaporation is determined by the temperature of the water, the temperature and pressure of the air, and the relative amount of water vapor in the air (humidity). Decreased humidity, higher temperature, or lower pressure increases the rate of evaporation, and *vice versa*. The presence of any solutes in the water retards evaporation. Likewise water adherent to any substance, or imbibed by it, is held there and evaporates less readily than if in contact with water particles only. Thus the water evaporates from a dish of wet sand or from a wet towel or sponge more slowly than from an equal surface of free water.

Since the actual exposed surface may be greatly increased by spreading out the water over sand grains or linen fibers, the evaporation from a given area of the *material* is not comparable with that from an equal area of water.

Because the evaporation from a green leaf and that from a like area of water are not equal is no reason for giving a special name to the evaporation from leaves, as has been urged. If it were, we should need one term for evaporation from a

towel, another for evaporation from a sponge, etc., for the rate varies always according to the material with which the water is in contact.

Adhesion. — The water which is part of a plant body adheres to the particles of cell wall, cytoplasm, and its inclusions, and is held with unequal tenacity according to the amount of each substance and its relation to water. As a rule, the greater the proportion of water in any substance, the less firmly it is held. The attractions between the water particles and plant substance are altered when the plant is "killed." Thus, if a living and a dead leaf be placed side by side in dry air, the dead leaf loses its water much more rapidly than the living one, and shrivels in a few hours. Probably this is in large part due to changes that the cytoplasm undergoes, which we call death; but these cannot be accurately described, beyond certain gross visible changes that do not help us to understand the matter.

Cytoplasmic changes. — There are many changes that the cytoplasm may undergo, which, though not visible, occur in the course of daily living. The nature of these changes is not known, and the precise way in which they affect water loss is not known. Some of them may be produced by the very diminution of the water content itself and thus at any moment may operate to alter suddenly the rate of evaporation.

A somewhat analogous action is known in the case of a number of salts which form hydrates with variable quantities of water. Thus, copper sulfate forms a pentahydrate, a trihydrate, and a monohydrate. In drying at 50° the pentahydrate ($CuSO_4$, $5H_2O$) maintains a vapor pressure of 47 mm. (mercury) as long as any pentahydrate remains; then the vapor pressure suddenly drops to 30 mm., that of the trihydrate ($CuSO_4$, $3H_2O$). With further desiccation it again suddenly falls, as soon as the trihydrate is all decomposed, to 4.5 mm., the vapor pressure of the monohydrate ($CuSO_4$, H_2O), and there it remains until all the water is driven off. In this case there would be at each point a sudden fall in the rate of evaporation. Just such sudden alterations have been observed in transpiration.

Regulation. — To say that the living protoplast "regulates" the loss of water from a plant is only to say that as the nature of the living material may change, its water relations change, and the rate of evaporation changes in consonance. But this is not "regulation" in the sense of adjusting the loss to the income, so that no harm may come to the plant. It is regulation only in the sense that the crystal, when heated, "regulates" the loss of its component water. In both cases evaporation becomes increasingly difficult, and for the plant this *may* avert death from excessive water loss.

Influx of water. — Transpiration has been called a function because it creates a current of water through the plant, which was falsely supposed to sweep in with it the needful mineral salts. But it is impossible to reconcile this conception with present ideas of osmotic movement. The only condition under which more water can enter is when, by the concentration of solutes in the plant, the internal pressure of the water of these solutions has been reduced; and this is precisely the tendency of evaporation. If the water and plant substance were in equilibrium, evaporation from aerial parts would upset this equilibrium by reducing the amount of water, which would be replaced by the entrance of water at any permeable region in contact with it. But this would by no means furnish an adequate reason for the entrance of any solute which was in equilibrium before evaporation took place. On the contrary, by concentration of the solution, the tendency would be in the opposite direction; the solutes to which the protoplasts were permeable would emigrate. And the mineral salts in question, being admissible by hypothesis, would do this. Transpiration, therefore, may occasion an influx of water, but not of salt; indeed it might easily cause an outgo of salts.

Transpiration and salts. — Transpiration has been called a function, also, because it was supposed to be useful in concentrating the dilute solutions of salts brought up to the leaves.[1] That evaporation of water from the leaves would tend to do this is true, of course. But the loss of water is at once compensated, under favorable conditions, by the entry of more water, and the solutions are again diluted. If equilibrium were assumed for the moment, then the disturbance of equilibrium by evaporation would determine a movement of water to readjust it, and the solution would again be brought to the same concentration. Were a liter of water containing a gram of cooking salt set on the fire to boil, and were pure water added as fast as it boiled away, no concentration of the salt solution could occur. But if salt solution were added as water evaporated, the concentration of the salt would be constantly increasing. This idea of the concentration of dilute solutions in the leaves by evaporation involves, therefore, the same assumption as the other " function " assigned to transpiration; namely, that water carries along with it the dissolved salts, as a river current sweeps along suspended mud. But this is a mere assumption, and contradicts both theory and observation of osmotic movement.

[1] One popular book for children even speaks of leaves as the plant's "kitchens," where the thin "soups" are boiled down.

A possible advantage. — There is only one region in the plant where solutes may move with the water; that is, where solutions move as a whole, namely, in the conducting tissue, which extends from root cortex to leaf cortex. But solutions cannot enter this tissue in the live plant without first passing through several live cells of the cortex, where osmotic movement only is possible; nor can they usually reach the evaporating surface of a leaf (the wet walls of the aerating passages) without passing several live cells, where again the solutes and water must move independently. (See movement of water, p. 341.) It is conceivable that the relatively rapid movement of solutions along this portion of the path from root to leaf may be advantageous to the plant by placing a greater supply of salts within reach of the leaves; but there is no proof that plants depend on this arrangement for an adequate amount of salts. Moreover, this is rendered improbable by the fact that many plants grow most luxuriantly with practically no transpiration for months at a time to set up such a stream of solutions along the conducting tissue.

A menace to life. — Transpiration, far from being a function of plants, is an unavoidable danger. That it is a danger, a real menace to life, is almost a matter of common observation. Millions of plants perish annually because the outgo of water is greater than the income. A loose soil and an exposed situation, sudden extreme evaporation due to a hot dry wind and a blazing sun, or prolonged drought, are causes of death only too well known to farmers in some regions. Scarcely a plant escapes the loss of some parts by reason of shortage in the water supply; and in temperate regions, with the average rainfall (say 100 cm. annually), few plants attain the development of which they are capable with a larger water supply. The luxuriant weed of well-watered ground compared with the same weed, meager and dwarfed on the dry wayside, illustrates what a menace to life and vigor is the evaporation from plants.

Transpiration and growth. — There are, of course, other causes of stunting and meager development than transpiration. If some of these operate to reduce vigor and growth, transpiration is affected thereby. In fact, growth and transpiration, in seedlings at least, seem to be reciprocally related, and the one varies directly as the other, when an ample supply of water is available, as in a water culture. It is not improbable that a like relation exists under these conditions in mature plants.

Transpiration unavoidable. — Dangerous as transpiration is, it is unavoidable, because moist cell walls must be exposed to permit solu-

tion and entrance of the gases absolutely indispensable to life. To be sure, the outer walls of the surface cells are relatively dry, especially in plants of dry regions, where water loss is to be reduced to a minimum. Of the total water lost scarcely more than 20 per cent, and as little as 3 per cent, escapes through the epidermis. This evaporation is sometimes distinguished as cuticular transpiration. The remaining 80–97 per cent diffuses through the stomata and constitutes stomatal transpiration. The efficiency of this arrangement in reducing transpiration and yet admitting gases freely is more obvious when one observes that the actual evaporation surface — *i.e.* of the cells bounding the intercellular spaces — is several times that of the leaf itself.

The place of maximum cuticular evaporation has been shown in some leaves to be that part of the outer wall of the epidermis where the side walls abut. In these cases water of imbibition is more abundant there than elsewhere.

It is impossible to determine the actual surface exposed in the very irregular air passages. If a leaf 1 mm. thick had an epidermis 0.1 mm. thick of coherent cubical cells on each face, and if the remaining cells were spheres each 0.1 mm. in diameter, tangent to each other, the internal surface would be about fifteen times the area of the corresponding outer faces of the leaf. This, of course, does not pretend to picture the actual state of affairs; but it will give an idea of the relative magnitudes involved.

Stomata. — The guard cells of the stomata are different from the rest of the epidermal cells in form, in the peculiar unequal thickening of their walls, and generally in the possession of chloroplasts. These characters and the position of the guard cells with reference to the adjacent subsidiary cells determine simultaneous differences in turgor and make them behave differently from the others. In general when turgid, they become arcuate, and when flaccid, they straighten. The mechanics of these movements differs considerably with differences of form, structure, and position, and in none of the several types that have been distinguished is it fully understood. The chloroplasts are supposed, but on no very good grounds, to impart power to make osmotically active substances that do not exist in adjacent cells (or are present in smaller amount), so that these cells may be more turgid than the others with the same water supply. The longitudinal thickenings are elastic and are supposed to straighten the cells when they become flaccid. The auxiliary cells are supposed to offer proper bracing for the guard cells so that turgor will arch them.

Regulation by stomata. — Naturally the guard cells are most likely to be turgid when the water supply is good; then the opening of the slit

between them permits free diffusion of the water vapor into the outer air. Conversely, the guard cells become flaccid with scant water, straighten elastically, and practically close the slit. This sort of adjustment is held to " regulate " the transpiration, permitting it when water is abundant, reducing it when the supply is inadequate. Yet if the assumption of the existence of special osmotically active substances in the guard cells were correct, they should be the last to feel the slackening of the water supply; and so one must assume further that they are adjusted to water much as are the other green cells of the leaf — an assumption which is hardly justifiable in view of their position and connections. Of course the immediate effect of the reduction in area of the stomatal slits is to reduce the amount of vapor diffusing through them. But this in turn would increase the relative humidity of the internal atmosphere (*i.e.* that of the intercellular spaces), would cause the accumulation of a " head " of pressure, so to speak, that would accelerate the diffusion through the narrower slit, and the system would tend to reach an equilibrium again. Thus the closure of the stomata is rendered partially or wholly ineffective. Were the internal atmosphere saturated with moisture when stomata are open (as has been assumed), the closure could not have this effect. But this assumption has not proved correct. Other changes in the external world (*i.e.* stimuli) affect the guard cells. Of these light is the most notable. In general the guard cells curve in light and straighten in darkness; the tendency, then, is for the stomata to open at a time when the evaporation is greatest and to close when it is least.

It is difficult to reconcile the facts with the commonly accepted view that the stomata are " delicately balanced valves " which adjust transpiration to the " needs " of the plant.

If the logic on which that idea rests were valid, it would prove rather that the stomata regulate the admission of gases, since any diminution of the size of the slit must diminish the amount of CO_2 admitted to the air passages, no " backing up " and accumulation of a " head " of pressure being possible in this case, whereas it does occur with water vapor diffusing from the plant. In the absence of any apparent advantage in regulating the movement of gases, and the " need " of some control over evaporation, it has been assumed that the stomata are able to adjust matters so that enough water will flow through the plant, carrying with it needed salts, while at any time these governors can check loss when danger threatens. Many cases, however, have been reported

in which the guard cells are immobile, or respond very sluggishly to external stimuli. Further, the more exact become the studies on plants of desert regions, where the need of an effective regulating mechanism seems most obvious, the less efficient do the stomata appear. Rather it appears that they are scarcely more than a tardily acting mechanism which may save the plant in extremity, but does not produce any exact adjustment.

Factors in transpiration. — The amount of water lost from a given surface of plant tissue is extremely variable. The humidity of the air, its temperature and pressure, which also affect humidity, and the temperature of the plant are the chief factors which cause the rate of evaporation to vary. The simplest mode of determining evaporation quantitatively is by weighing potted plants at intervals, having prevented evaporation from the surface of pot and soil by some impervious covering of rubber, metal, or wax. It is not justifiable, however, to apply these data to plants in nature.

Humidity. — In a saturated atmosphere there can be no water loss. Yet experimentally this is very difficult to establish. The reason is to be sought in two directions. First, it has been found practically impossible to maintain an atmosphere absolutely saturated at all times, for that means an invariable temperature, which, under other conditions necessary to the experiment, is unattainable. Second, even were the proper external conditions attained, the plant by respiration would be a little warmer than the air, and the air next the plant, therefore, would not be quite saturated; so some small amount of evaporation might take place. Yet during rain, mist, or fog, practically no evaporation occurs; and as the humidity decreases from 100 per cent to the 70 per cent of a moderate day or to the 50 per cent of a dry day, evaporation increases. As the humidity fluctuates from day to day or even from hour to hour, the evaporation varies likewise. The most marked changes in relative humidity are due to the rising or falling temperature of the air. As temperature rises, relative humidity becomes less, the heat energy imparted to the plant is greater, and evaporation is increased by both causes.

Barometric pressure. — As the air pressure is reduced the boiling point of water falls; so fluctuations in the barometer indicate inverse changes in the rate of transpiration. Yet these variations at any locality are insignificant; the reduction in air pressure becomes important only in comparing plants at high and low altitudes. In alpine regions, where

low barometer may coincide with low humidity and therefore intense light, the excessive evaporation often becomes a powerful factor in dwarfing plants and in controlling their distribution.

Temperature. — The temperature of the plant itself tends normally to equal that of the air, since its extended surface permits quick gain or loss of heat toward equilibrium. A rise of temperature in the air, therefore, is quickly followed by a rise of temperature in the plant, and (even with no change in the relative humidity of the air) by increased evaporation. But the temperature of the plant depends also upon the energy absorbed by the green pigment in diffuse light or direct sunlight. In diffuse light the greater part of this energy is used in food making, and only a small portion exerts a heating effect. But in sunlight two thirds to three fourths of that absorbed is free to heat the tissues, and as soon as that begins, evaporation is thereby much accelerated. This tends to dissipate the heat.

It has been proposed to call the evaporation due to the excess of energy absorbed by the chlorophyll, *chlorovaporization*. The term has its only value in promoting recognition of the fact; but chlorovaporization cannot be distinguished practically from the rest.

Were it not for this transfer of energy to the water vapor, the temperature of the tissues would rise to the danger point, or at least to a degree which retards food making. When transpiration is greatly reduced by enclosing a shoot in a glass chamber whose air quickly becomes nearly saturated while the light is absorbed, death quickly ensues. The "scalding" of leaves by sunshine after a summer shower is an example of the same effect. If a plant derives no other advantage from transpiration, this prevention of injury by overheating in direct sunlight is certainly one. For even temporary interference with food making might be serious, and permanent stoppage of it by the killing of any considerable area of leaves might be fatal to the whole plant. However possible it might be for plants to meet this difficulty by other methods, if transpiration could be eliminated for other reasons, under the present organization transpiration is of real advantage in this particular.

Amount transpired. — Because of the extreme variation, from zero to the maximum, a quantitative statement of the amount of evaporation is of little value, though a voluminous literature records an enormous number of observations and calculations. The following will serve as illustrative examples.

MEASURED EVAPORATION FROM 100 SQ. CM. OF LEAVES (200 SQ. CM. OF SURFACE) IN BRIGHT DIFFUSE LIGHT, AT ABOUT 20° C., WITH HUMIDITY ABOUT 50 PER CENT

	1 hr.	24 hr.
Phaseolus vulgaris	0.117 gm.	2.81 gm.
Hedera Helix	0.17	4.09
Begonia argentea	0.19	4.57
Coleus Blumei	0.211	5.06
Cucurbita Pepo	0.224	5.39
Ficus elastica	0.262	6.3
Helianthus annuus	0.5	12.0
Lupinus albus	0.594	14.27
Chrysanthemum frutescens	0.681	16.35
Vicia Faba	0.683	16.4

Hemp plants in a season of 140 days were estimated to evaporate (each) 27 kg. and sunflowers 66 kg. of water. It is estimated that if the water evaporated by the following cereals were again condensed on the area occupied by each sort, say 1 sq. m., it would cover the ground in the case of rye to a depth of 83 mm., wheat, 118 mm., and oats, 127 mm. The average annual rainfall in the north central states is in the neighborhood of 1000 mm., so that one twelfth to one eighth of the total passes through such cereals.

A birch tree with 200,000 leaves is estimated to evaporate on a hot day 300 to 400 kg. A beech, 15 years old, is said to average about 75 kg. per day in the months from June to September, inclusive. At that rate a hectare of beech forest containing 400–600 trees would evaporate some 20,000 barrels. In all these calculations and estimates a liberal allowance must be made for errors.

Reduction of water loss. — Among all the agencies that affect the form and mode of development of plants none has more influence than water, and the relation between the available supply and the loss by evaporation. In the peculiarities of form and structure which seem related particularly to water, many see "adaptations" to a habitat with much water, a moderate amount, or a scanty supply. Thus the cutinization of the epidermis, the formation of a waxy or resinous coating, and the development of cork are structures which reduce the loss of water. In other plants the scanty or fleshy foliage, the complete absence of leaves, the development of water-holding tissues, the short cylindric or globular fleshy body, the deep-running roots, and many other peculiarities (treated more fully in Part III, Ecology) are considered as "adaptations" to a dry climate. It would be better to look upon them as effects of climate and similar factors, since experiments indicate that such "adaptations" can be produced at will, even in one generation, by cultivation under appropriate conditions.

2. EXUDATION OF WATER

Forms of exudation. — Besides the vapor which constantly exhales from plants, liquid water exudes from certain regions intermittently. The places whence it issues are, first, certain specially permeable areas of the permeable regions in an uninjured plant; second, the conducting tissue when opened by some wound. *Guttation* is the escape of water in drops from uninjured plants. It occurs especially in leaves in the vicinity of the tips of main veins, where there are stomata, often enlarged, called water pores, through which water exudes. *Bleeding* is the oozing of water from the water-conducting tissues when ruptured. It is especially notable in the spring, before the foliage is fully developed. *Secretion* consists in the exudation of water and solutes from certain specialized cells, constituting a gland, and found on various parts of plants, but especially on foliage and flower leaves. All these processes are essentially similar, with minor differences.

Guttation. — Guttation may be readily observed by inverting a glass jar over grass seedlings growing in well-watered soil and thus checking the evaporation. In a short time a water drop accumulates at the tip of the blade and enlarges until it runs down or falls off. Leaves of vigorous plants of many species (*e.g.* aroids, fuchsia, cabbage, nasturtium) under like conditions show droplets of water at the tips, or at marginal teeth, or near the end of main ribs.

Accessory structures. — In all these cases an examination shows essentially the same features: (*a*) a rift in the epidermis, or one or more water pores, over (*b*) a rather large chamber, which is bounded by (*c*) more or less specialized colorless parenchyma cells (*epithem*), and near by (*d*) the tracheids at the end of a vein. The rift in the epidermis may be due (as in grasses) to growth and consequent stretching and rupture. The water pore is simply a deformed stomatal apparatus whose dilated slit is always wide open because the distorted guard cells are no longer motile. When the water pore is single, it is usually greatly enlarged and deformed; when there are a number together, each is more nearly like an ordinary wide-open stoma. The cells lining the substomatal chamber differ from the mesophyll cells chiefly in lacking chloroplasts. They resemble the sheath of colorless cells, the so-called transfusion tissue, that adjoins the tracheids, which form the endings of the water-conducting bundles of the leaves. In some cases this epithem seems to be a water-secreting

tissue and to deserve the name water gland; in others it seems to be passive.

Guttation in fungi. — Guttation is not confined to the higher plants, nor are there always such elaborate accessory structures. It occurs in its simplest form in many fungi. Thus *Pilobolus crystallinus* owes its specific name to the droplets of water which appear on its sporangiophores (fig. 630), and *Merulius lacrymans*, the dry-rot fungus, likewise, "weeps" so much water that it accumulates in big drops on the surface of its sheetlike mycelium.

FIG. 630. — Sporangiophore of *Pilobolus*, showing exuded water. — Adapted from ZOPF.

Nightly guttation. — In nature the checking of evaporation, which results in guttation, occurs chiefly at night, when many young plants exude water. What remains adherent at the water pore may be partly resorbed when transpiration begins.

This seems to be the way in which a destructive bacterial disease of cabbage infects the plants. By contamination of the hanging drop the bacteria find their way into the chamber as the drop evaporates or is resorbed, there develop and so kill the adjacent cells, whence they enter the xylem bundles and work backward, killing and rotting the bundles. When the crop is gathered and stored, they develop further, until the head is spoiled by the extension of the blackened and rotted tracts in the blanched leaves.

One may easily observe the exudation of water from the leaves of lawn grasses early in the evening, when the "dew" is said to be "falling." The warm soil conduces to the entry of water; the cooler air checks evaporation; these conditions permit maximum turgor; guttation at the tips of uninjured leaves, or, more often and more promptly, bleeding from the cut ends of the leaves is the result. Dew, of course, may form under proper conditions; but exuded water forms a great part of what passes as dew.

Artificial guttation. — Guttation may be produced artificially by injecting water under pressure into the stem of a plant known to have water pores, as by attaching the end of a cut shoot to a water tap. Presently droplets exude at the usual places. It is usually assumed that the water is thereby forced through the plant tissues, but as city water pressure varies from 2–3 atmospheres (seldom more, and less will often answer), it is doubtful if so low a pressure (as compared with the 3–10 atmospheres of common turgor pressure) would be adequate to do this (see further, p. 336).

Quantity exuded. — In a few plants, especially in aroids, guttation under favorable conditions is so rapid that water drips from leaf tips or is even ejected. Thus a vigorous leaf of *Colocasia* has yielded 1008 cc. of water in 9 days, the water dropping at the rate of 85–100 drops per minute at times. *C. nymphaeoides* has been observed to eject a stream of minute droplets (at a rate of 195 per minute, so that it seemed almost a continuous jet of water) to a height of about 1 cm.

Advantage? — Seeing the structural features which permit guttation, one naturally asks, Is it advantageous? To that question no certain answer can be given. It is assumed that the free escape of water at these points prevents its escape elsewhere, and therefore prevents the infiltration of the aerating system with water, which would greatly retard the entry of gases and so the manufacture of food. But there are so many plants which lack the arrangements for guttation that one must doubt if this answer be adequate.

Bleeding. — Bleeding may be observed when vines are pruned rather late, or in many cases when a potted plant is decapitated. It must be distinguished from exudation due to heating the water and especially the gases contained in the woody parts of a plant, which has the same general effect. Thus, when a green stick is put on the fire, the scanty sap presently boils out of the ends; for the expansion of the gases and of the water, and later the steam generated by the fire, drive it out forcibly. Or if on a cold day in winter, one bring into a warm room a branch of a shrub or tree, water will soon ooze out at the cut surface. Here the gases in the wood are warmed (for though fuller of water in winter than at other times, the wood is never free from gases, else no green wood would float); they expand, and press upon the free water, forcing it out at the nearest opening. True bleeding, however, is restricted to live plants and is quite independent of any gas pressure due to heat.

Industrial applications. — Collecting maple sap for sugar or sirup making is partly an industrial application of bleeding. The work is often begun when only the heating of the twigs on a warm sunny day is active in forcing out the water through the wound made in the trunk; but a great part of the later exudation is dependent on other causes and must be accounted to this extent as true bleeding. Another commercial application of bleeding is found in the collection of the sap of various species of *Agave* in Mexico and Central America for the manufacture of fermented and distilled liquors. The process begins with cutting out the huge bud at the time when the plant, at the end of 5–15 years' growth, is about to send up the great flower stalk, 12–20 cm. in diameter and 6–10 m. high. Into the basin formed by removing the bud, the plant exudes several liters of water a day, for two months or more; this is collected daily, and after the addition of milk and fermentation is esteemed as a beverage, called *pulque*. Extensive plantations are devoted to rais-

ing the agave or maguey, and pulque trains run into the large cities, as milk trains do in this country. The fermented sap is also distilled to make various fiery alcoholic drinks.

Conditions. — The conditions under which bleeding occurs are like those for guttation, a liberal water supply and limited transpiration; that is, the conditions which permit maximum turgor. Even so, not all plants bleed; hence it cannot be at all necessary, nor can the causes be universally active.

Cause of exudation. — The cause of bleeding and guttation is to be sought in the development of high turgor in certain cells (on account of the osmotic pressure of the solutes in them to which the protoplast is impermeable), which is made possible by adequate water supply. To stop evaporation by making the air about the aerial parts very moist, or by cutting away the aerial parts, or to have limited evaporation because the foliage is not yet fully developed, are merely ways by which a water supply, that might otherwise be barely enough to cover the evaporation, is made ample; and this permits high turgor when other conditions are met. When the turgor rises to a certain point in the active cells, it seems that water is exuded.

This may be mere filtration under pressure. But we may also conceive it to be due to a sudden alteration of the permeability of the cytoplasm, wrought by the very pressure itself. In that event, upon the relief of pressure when the outgo occurs, there would be a gradual recovery of impermeability and consequently of turgor to the maximum; then another automatic change of permeability, a consequent outrush of water, and so on.

This outflow naturally cannot be pure water; but on the theory of filtration the water will contain at least the substances to which the protoplast is permeable; and on the second hypothesis, any or all solutes might be released, the sap as a whole escaping. In the water there are often substances in small amount, regarding whose osmotic relations we are ignorant, though the general assumption is that they could not pass the cytoplasm without some special modification of its permeability. When that is demonstrated, it will be necessary to adopt the second hypothesis, which is also used to account for the presence of such substances in secretions (see p. 340). Until then it will suffice to assume that they issue with the water because they are free to do so.

Tissues concerned. — In the case of *Pilobolus* and like plants, the turgor which causes the escape of water evidently arises in the very cell or

coenocyte from which it escapes. This may also be the case in guttation among seed plants. The epithem of the water chamber, receiving an adequate supply of water from the adjacent vein, may develop turgor sufficient to cause water to pass the cytoplasm and the wall. It is obvious that to issue from the free surface it will encounter less resistance than elsewhere; consequently it takes this direction. The chamber fills and water soon oozes from the water pore. But the epithem cannot develop an adequate turgor unless the water supply is sufficient. That may be made sufficient either by checking the transpiration, or by forcing water up to these cells so that they may get enough, even though transpiration is unchanged. Water may be supplied thus artificially by cutting the stem and attaching it to a water tap; or the same end would be accomplished in nature if the root cortex had a supply adequate to enable it to become fully turgid and exude water under pressure into the conducting system.

"**Root pressure**." — The condition just mentioned often exists in the root cortex, and perhaps always when plants are not flaccid. The location of this turgor has suggested for it the name "root pressure." This is unfortunate, because it tends to obscure the fact that any live thin-walled cells with like conditions may develop a turgor which will cause water to exude. Thus, bleeding was found to occur in the inflorescence of some tall palms, but the root cortex had no part in so distant an exudation; the pressure originated near the base of the flower stalk. The "root pressure" being a frequent cause of bleeding, the phrase "bleeding pressure" has been suggested as a substitute; but this is little better, since whether or not bleeding results is purely incidental. No special term is needed other than turgor pressure; that is general and is specific enough. (See also p. 349.)

Amount and pressure. — Experiments on bleeding are often conducted with potted plants, which are decapitated, and to the stump is affixed apparatus for measuring the amount of water exuded, or the pressure with which it is forced out. With trees, the trunk is bored and the receptacles or gages attached. A few examples will give an idea of the maximum quantity of the sap and the pressures involved.

A calla lily bled 39 cc. in 24 hours. A vigorous European grape sometimes exudes nearly a liter per day. The Mexican agaves, cultivated for this purpose, are said to give out 5–6 liters daily for several months. Under favorable conditions, the sugar maple yields 5–8 liters in the course of a day, and the birches give out about as much.

The pressures, recorded in millimeters of mercury (760 = 1 atmosphere), vary from 0 to

Ribes rubrum (red currant)	358
Acer platanoides (sycamore maple)	347
Acer saccharum (sugar maple)	1033
Psedera quinquefolia (Virginia creeper)	615
Betula alba (white birch)	1390
Betula lutea (yellow birch)	1815
Betula lenta (black birch)	2040
Vitis vinifera (European grape)	860

Much study has been given to variations in the amount and pressure of bleeding; seasonal and possibly diurnal fluctuations have been discovered; but inasmuch as turgor pressure must be influenced by transpiration, itself of infinite variability, the precise results of these studies are not important.

The limited movement of water through submersed aquatics which has been described cannot be due to transpiration, and is probably not a case of guttation. The experimental evidence is scanty and the movement may be referable to the larger heating effects on the leaves as compared with the stems. This should create a slow movement of water out of the leaf, to be supplied from below.

Secretion. — Secretion is a much more general and varied phenomenon than guttation or bleeding. It is performed by more limited and specialized tissues, called glands, and the variety of substances which escape is much greater, though the amounts lost are much smaller. Many of the secretions are of such a nature that they play an important part in the life of the plant; others are of no use so far as we know and are therefore called waste products. No distinction can be made in plants between useful secretions and waste excretions.

FIG. 631. — Young glandular hair of *Pelargonium*: *c*, cuticle; *o*, volatile oil. — From PART III.

Glands. — There are some glands which secrete water, with no distinctive solutes, like that which escapes in guttation and bleeding; and because there are no distinctive solutes these are called water glands. Glands are named usually according to the most abundant or characteristic material they secrete. Thus those in whose secretion calcium salts become conspicuous by concentration are called lime glands; digestive glands secrete water containing enzymes. Most common of all are the nectar glands or nectaries, abundant in flowers, but found also on other parts as extra-floral nectaries (fig. 1183), whose

water is sweet with sugar and often fragrant. Not all glands, however, secrete water and its solutes. There are glands whose secretion is an essential oil,[1] of which a great variety are formed. Still others secrete resin, which may be formed from an essential oil.

Form of glands. — The form of glands is various. A single epidermal cell may differ from its neighbors; it may be level with them, or sunk, or raised upon a shorter or longer stalk, like the glandular hairs (fig. 631). A filament or a cluster of such cells may form a stalked gland (fig. 632); the gland cells may form a rather indefinite mass, or they may line a shallow cavity (fig. 633), or a deep pouch, as in the nectary of the nasturtium (fig. 634); or they may be the epithelium of a simple or branched duct, as in the lilies (fig. 635). Nor do all glands pour out their secretion on the surface. The gland cells may part when young, forming intercellular spaces into which the secretion exudes to escape through water pores. Or a single intercellular space may develop in the center of the group (fig. 636) which receives the secretion; then as the gland and space grow, the secreting cells form an epithelium for a closed reservoir, larger or smaller, containing the secretion. Or, later, by the destruction of the gland cells loaded with the secretion, it finally occupies their place as well as the intercellular space, and reaches the surface only by mechanical rupture of enveloping tissues (fig. 637).

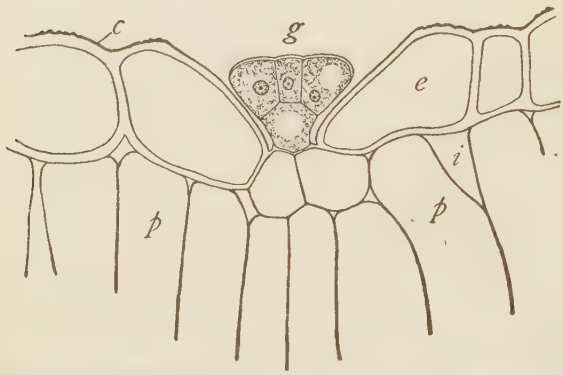


FIG. 632. — Gland (*g*) from the upper surface of the leaf of lilac (*Syringa vulgaris*): *e*, epidermis; *c*, cuticle; *p*, *p* palisade cells; *i*, intercellular space.

Emission of secretions. — Very little is known of the chemical processes by which the peculiar materials of the secretion are formed. Each sort of gland doubtless pursues a different course. Nor is it possible to account for the emission of the various substances. Some, like

[1] Not true oils, from which they may be distinguished by making only a transient grease spot on paper.

cane sugar, are known to be retained ordinarily by the cytoplasm; yet nectar glands secrete sugar one or more times. Others, for example enzymes, have a composition which, though imperfectly known, is such as to suggest that the cytoplasm would usually be impermeable to them; yet digestion occurs in such places as to make it certain that enzymes are able to pass out of the cells in which they arise.

FIG. 634. — Flower of nasturtium (*Tropaeolum majus*) cut through the middle to show the spur (*s*) and the nectar (*n*).

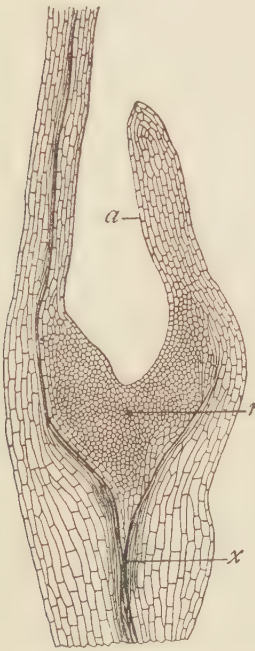


FIG. 633. — Section through a petal of buttercup (*Ranunculus*), showing nectar gland (*n*) and shallow receptacle formed by the "nectary" (*a*). Note bundle of conducting tissues (*x*). — After BONNIER.

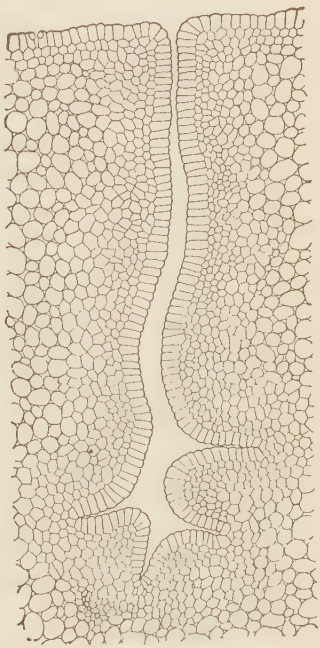


FIG. 635. — Nectar gland in the ovary of day lily (*Hemerocallis flava*). — After SCHNIEWIND-THIES.

The problem, therefore, is: How can solutes pass the ectoplast usually impermeable to them? The answer is merely in the form of a hypothesis, like the one already proposed to account for guttation and bleeding. If the accumulation of the solute causes a rise of turgor, it is conceivable that the very pressure itself might work such a change in the cytoplasmic membranes that they alter their permeability and permit the outrush of water and its solutes in the direction of least resistance, which will be toward the free surface. Whether a renewed secretion will take place depends on the further activity of the cell. Given a repeated formation of the secretion, it might escape again. The hypothesis then suggests a rhythmic variation in the permeability of the cell membranes, the secretion being formed inside the cell.

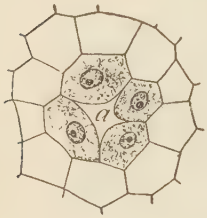


FIG. 636. — Young resin gland of fir (*Abies*): *a*, duct, an intercellular space formed by the separation of the four nucleate cells. — After TSCHIRCH.

This hypothesis is clearly inapplicable to secretions which are not miscible with water, like essential oils and resins. They are probably formed, however, in the very wall itself, and thus the material may not have to traverse the ectoplast as resin or oil. Unfortunately, even the place of their origin is still obscure.

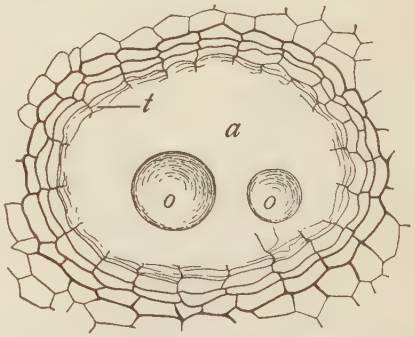


FIG. 637. — Oil receptacle (*a*) in orange (*Citrus Aurantium*), formed partly by splitting, but chiefly by destruction of secreting cells and their neighbors (*t*); *o*, *o*, drops of essential oil. — After TSCHIRCH.

Rôle of certain secretions. — Nectar is gathered by many insects, some of which store it, after partial digestion, as honey. While the floral glands are being explored for nectar, the visitors become dusted with pollen and transfer this to ripe stigmas of the same or other flowers, thus insuring pollination in many cases where otherwise it might not occur (see Part III on pollination). The rôle of extrafloral nectar is not clear. Digestive glands, most definite in insectivorous plants (p. 386), secrete enzymes (p. 399) by which the soft parts of captured insects are dissolved. Essential oils (p. 413) sometimes prevent plants from being eaten by animals.

3. THE MOVEMENT OF WATER

Transpiration stream. — In the two foregoing sections it has appeared clearly that the region where water enters a plant and the region whence it leaves are rarely identical, but that these parts are more or less widely separated. There must be, therefore, movement of water through the body. Small quantities of water are used in the body for saturating new-made materials and parts, and for food making by green plants. Somewhat larger quantities are exuded by guttation, bleeding, or secretion. But the dominant cause of movement is to be found in evaporation, for the amount thus leaving the body is often many times greater than all other quantities combined. So considerable is it that the flow through the body is figuratively known as the transpiration stream.

Transfer in small plants. — In the smaller land plants, whose bodies are composed of living cells throughout, as in many liverworts and mosses, the water has to travel but a short distance, and the movement can be osmotic only. Evaporation at an exposed surface concentrates the solutions in those cells, thereby reducing the internal pressure of the water, which moves from an adjacent cell to reestablish equilibrium, and so the disturbance soon reaches the surface cells in contact with free water, which enters the plant.

Origin of a conducting system. — We might infer that these osmotic movements are too slow to afford a proper supply to larger plants, because, as an actual fact, they are in operation for only relatively short distances; the larger the plant and the more necessary a large supply of water, the more perfect and extensive becomes the special system of tissues for conducting water by avoiding osmotic transfer. This is especially striking when one follows the development of such a plant as a sunflower from the embryo, a stage when there is no water-conducting tissue, to maturity, observing how the extent and amount of this tissue increases as the foliage develops and so increases the evaporating surface. It may be assumed that somewhat similar has been the history of the evolution of land plants. As the early aquatics became more and more exposed to evaporation, there probably came about the development of structures which limit the water loss, and simultaneously the development of the water-conducting strands, which greatly facilitate water movement.

Elongation of cells. — Presumably one of the simplest expedients to accelerate movement is to reduce the number of membranes which the

water must pass osmotically. This could be accomplished to a certain extent by elongating the cells in the main direction of travel; and it may be that elongation of the cells was one of the early steps in the evolution of a conducting system. To-day there are plants in which such strands exist, as in the stalk of the sporophyte of liverworts and mosses, and these are often accounted rudimentary conducting tissues.[1]

Lignified tracheids. — The complete elimination of the cytoplasmic membranes may well have been a second step in evolution. This would make movement more easy by removing just so much resistance from the path. If in addition the walls were altered so as to be more freely permeable to water, movement would thus be further facilitated. That change, known as lignification, is indeed common. Then by thickening the wall only in parts, leaving the rest thin, passage of water through it by way of the thinner areas would be still easier. Strands of elongated cells of this sort constitute the endings of the conducting system in the leaves of almost all plants, and they form almost the whole of the characteristic wood in gymnosperms and the conducting strands in pteridophytes.

Tracheae. — One further step attains the condition in the most perfectly developed conducting tissues, namely, the resorption of the greater number of the transverse partition walls between the elements, forming cell fusions of great length, known as ducts, or vessels, or *tracheae*, the latter from their occasional resemblance to the human trachea and the air tubes of insects. Resorption does not usually occur near the endings of the strands in the leaves; and in gymnosperms it fails except in the primary strands. But the other changes do occur, and the elements being cells and not cell fusions are distinguished as *tracheids*. Following the history of any row of cells which is to become a duct, there is first the elongation of the cells; then the unequal thickening of the wall and its lignification, together with the resorption of most of the end walls; and finally the disappearance of the protoplasm. Some such steps as these may also have marked the evolution of the conducting system through earlier ages.

Xylem. — The conducting system in the larger plants now consists of a series of strands known as *xylem strands* or as the xylem regions of the vascular bundles (p. 242). Physiologically it is more satisfactory to treat the xylem as independent of the phloem (p. 242), for although they are usually closely associated in their course, they may be independent, and the functions of the two are quite unlike. The xylem strands form a

[1] This is based too much on analogy and inference; the experimental evidence is weak.

connected series, extending from the root-hair region to the mesophyll of the leaves, among which they branch so extensively that there is scarcely a cell which is separated from a strand by more than a half dozen of its neighbors. Here the first branches end blindly (fig. 638) or join their fellows. A section of the root in the root-hair region shows likewise that only a few cells intervene between the free surface and the young xylem strands, which, nearer the root tip, are being differentiated from the plerome (p. 239). Like-

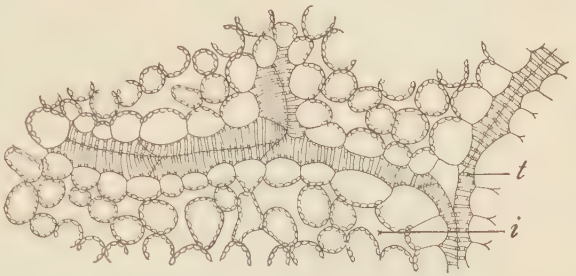


FIG. 638. — Ending of a xylem strand among the cells of the mesophyll in a leaf of lilac (*Syringa vulgaris*): *t*, tracheid; *i*, intercellular space.

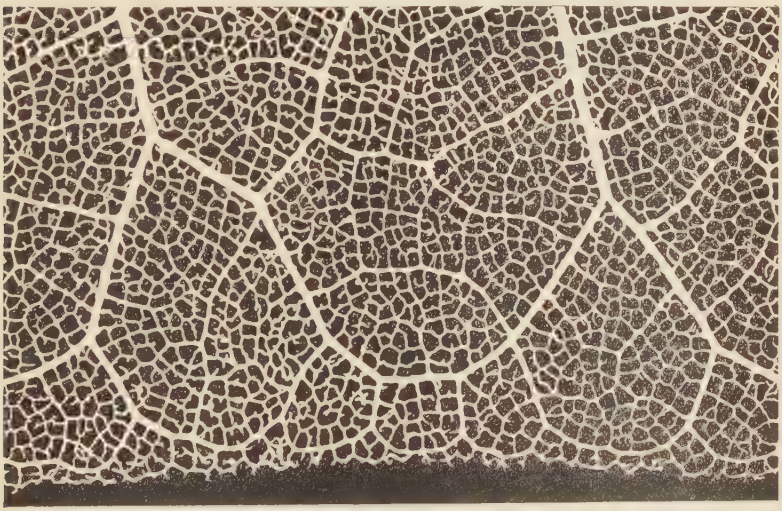


FIG. 639. — Skeletonized edge of a leaf of a *Ficus*, showing the mode of branching of the smaller ribs; the smallest are completely gone. — From a photograph by LAND.

wise, a section of the leaf (fig. 627, p. 319) shows the relations of this water-conducting tissue to the surface, and an examination of the venation of various leaves (of which only the larger veins are visible to the

unaided eye) shows how extensive is the branching (fig. 639). Between these extremes the bundles run, with lateral connections here and there, especially at the nodes, and more or less variation in size and branching.

Tracheal markings. — The walls of the tracheae are always peculiarly thickened, the thick regions being in the form of rings, or spirals, or a network (figs. 640, 641). The thin parts may be more extensive than the thick, as in annular and spiral tracheae (figs. 640, *a*, *s*; 641, *s*); or they may be mere spots in the midst of the thick wall, as in pitted tracheae (figs. 640, *p*; 641, *p*, *r*). The thick and thin parts in adjacent tracheae or tracheids correspond; and thus the movement of water laterally, when conditions require it, is facilitated.

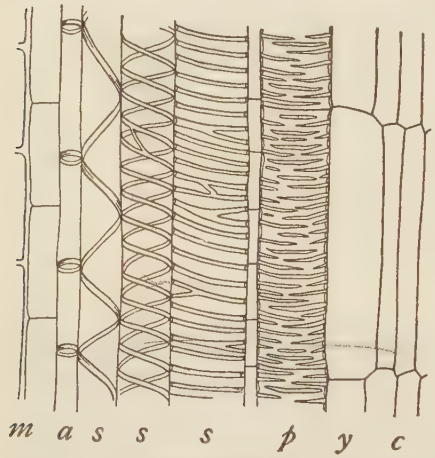


FIG. 640. — Longitudinal section (diagrammatic) of a young xylem strand: *c*, cambium; *y*, young trachea, undifferentiated except as to size; *p*, pitted trachea; *s*, *s*, *s*, spiral tracheae; *a*, annular trachea; *m*, pith. — After HABERLANDT.

In scalariform tracheids the parts of the wall not thickened are resorbed, and the neighboring cavities communicate freely.

If water in which some cinnabar has been rubbed up be passed through filter paper, to remove all but the very finest particles, and then the filtrate is driven under pressure through a piece of fresh pine wood, the pits become choked with cinnabar, showing that water filters through them more easily and so in greater quantity than elsewhere.

Secondary thickening. — The primary xylem, *i.e.* that differentiated from the young tissue near the growing points (fig. 642), is adequate to supply only the first leaves. As with age the foliage increases, each primary xylem strand may undergo secondary thickening; *i.e.* it has added to it similar tissues, originating from a layer of dividing cells which adjoins its outer face (fig. 643). In addition, this meristem (cambium), arising between the primary strands, may originate new strands of xylem tissue between the primary ones. These secondary strands may then increase in thickness in the same manner as the primary

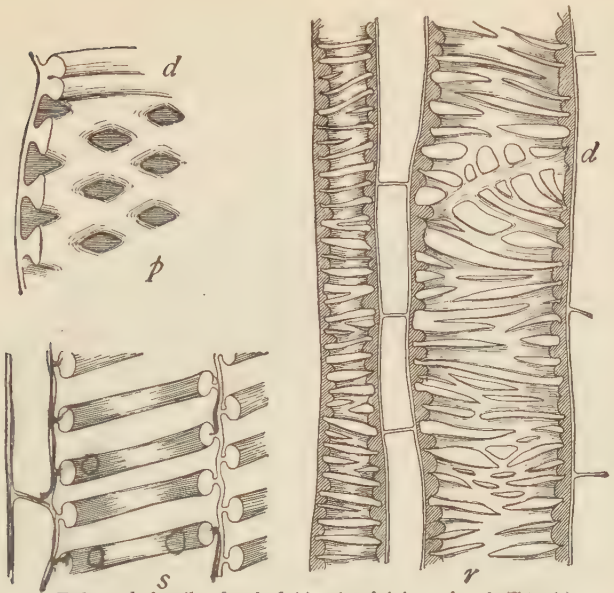


FIG. 641. — Enlarged details of spiral (*s*); pitted (*p*), and reticulate (*r*) tracheae; at *d*, traces of original partition walls. — Adapted from HABERLANDT and TSCHIRCH.

ones. When numerous primary and secondary strands are produced, they may form a column of xylem, with pith in the center, interrupted by thin radiating plates of parenchyma, the pith rays. Such is the condition in the sunflower, castor bean (fig. 644), and many other dicotyledons.

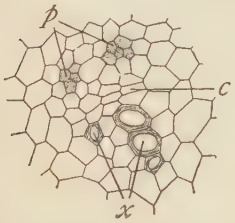


FIG. 642. — Young vascular bundle: *p*, primary phloem; *x*, primary xylem; *c*, first divisions of cambium cells. — After BONNIER. Diagrammatic.

In case the xylem strands do not undergo individual secondary thickening (as is the case in most monocotyledons), there may be a cylinder of meristem which repeatedly produces new bundles, as in asparagus. But in all plants which produce numerous leaves the increasing evaporation is

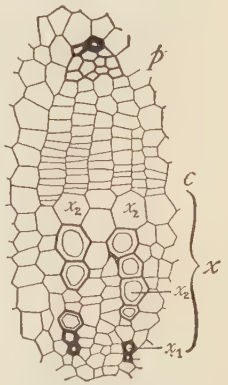


FIG. 643. — Older vascular bundle, with secondary thickening in progress: *p*, phloem; *c*, cambium, forming by division both secondary phloem and xylem; *x*, xylem, composed of x_1 and x_2, the primary and secondary xylem. — After BONNIER.

accompanied by an increase of the conducting tissues (see Part I, p. 243).

Annual thickening. — In trees and shrubs the xylem undergoes secondary thickening in the first season of growth, and this is resumed in the second season, and so on, from the persistent cambium. Thus arises a great cylinder of xylem, which constitutes the wood of the trunk and

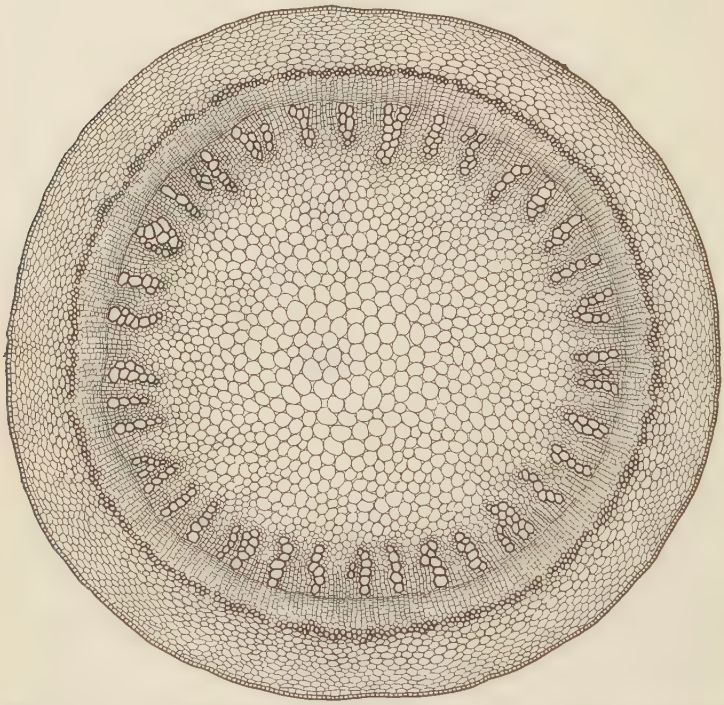


FIG. 644. — Cross section of stem of *Ricinus communis*, showing ring of secondary xylem; for description, see fig. 541. — From PART I.

branches. In many trees the xylem formed in the course of the growing season gradually changes its character. The first formed tissues contain many large ducts and less mechanical tissue, while the later formed xylem has small ducts and much mechanical tissue. In these cases the open tissues produced in the spring abut on the denser ones last produced in the summer or autumn, and the sharp contrast marks visibly the periodicity in growth. As these differences in the tissue depend upon growth, and as this is most affected by the annual seasonal changes, the growth rings are usually annual rings, and make possible an estimate of

the age of the tree. But annual rings may show subordinate rings, due to some pronounced climatic change which affected the rate of growth more than once in the year. These rings may be so pronounced as to make the age estimate uncertain, but in temperate regions the annual rings are usually well defined. In some trees the differences between spring and autumn wood are slight, and the annual rings are discerned with more difficulty. The definite annual rings are responsible in large part for the " grain " of wood. (See also Part III on annual rings.)

Heart wood and sap wood. — With age the xylem loses its capacity to conduct water, and sooner or later may so change in color and composition as to distinguish the older heart wood from the newer sap wood. These changes, however, do not coincide with the annual rings, nor do they exactly correspond with the differences in conductivity, since in some plants the whole of the sap wood, but in others only the youngest portion of it, is traversed by the transpiration stream.

Xylem is water path. — The evidence that the xylem is the path of the transpiration stream rests in part upon direct observation, but mainly upon inference from the effects of cutting the xylem strands or blocking the tracheae.

Relative development. — In the first place, one finds a general relation between the amount of transpiration and the development of the xylem. In most submersed water plants the xylem is very poorly differentiated, its place being occupied by some elongated cells, slightly different from their neighbors, which are morphologically equivalent to xylem, but physiologically they are negligible. On the other hand, in climbing plants, whose spread of foliage is large and their stems slender, the xylem reaches its best development, occupying a large proportion of the cross section of the stem, and having ducts of relatively large diameter. Not much reliance could be placed upon such a loose and general relation, were it not for more direct evidence.

Girdling. — Girdling experiments show more clearly the path of the water. It is a matter of common knowledge that by cutting through the sap wood of a tree the foliage promptly wilts and dies; and in earlier days it was commoner than now to see the trees in some piece of woodland " girdled," preparatory to clearing the ground for cultivation. But removing only the bark does not produce wilting, except after weeks or months, for thus only the phloem strands are interrupted. More exact experiments may be performed. By selecting a herbaceous plant whose vascular bundles are distinct, one may cut the pith, the vascular

bundles, and the cortex in different specimens and compare the effect. It will be found that only in the specimens whose bundles have been cut do the leaves wilt, and the fact that in woody plants the bark may be removed without causing wilting eliminates the phloem strands. Such experiments permit the inference only that the xylem strands are the chief paths of the transpiration stream, not that they are the sole path; for wilting implies merely an inadequate water supply.

Water moves in the lumina. — But the path can be localized more exactly. A shoot of a climber, such as *Clematis*, may be cut off under water, and the end sliced very obliquely, so as to open wide the ends of the ducts. If this shoot be fastened to a microscope slide, and the end covered with water, into which has been introduced some finely divided carbon, as from Chinese ink, one may watch the water swirling into the open ends of the ducts, its course being made evident by the opaque particles it carries. Under such circumstances it is evident that the water enters and probably traverses the lumen of the trachea. But this was for a long time a disputed point. When the extraordinary freedom of movement of water in lignified tissues was discovered, it was held that the water traveled in the substance of the walls and not in the *lumina* (the chambers they enclose). This opinion, however, rested upon inaccurate experimentation.

Closing the lumina. — Attempts were made by compressing the stem in a vise to collapse the tracheae, and so to close their lumina. In the earlier experiments of this sort, wilting did not occur, and the inference was plain, therefore, that the water traveled in the wall itself. Repeated studies showed that the difficulty of compressing the tracheae had been underestimated, and that when they were actually closed mechanically, the leaves did wilt. A better method of closing them is by plugging them with paraffin or gelatin which melts at a low temperature. By cutting a shoot under the melted material, it is carried up instantly to some distance in the tracheae. When cooled, it solidifies and a fresh surface of wall can be exposed by removing a thin slice, while the lumina remain plugged. The leaves of such a shoot promptly wilt when exposed to dry air.

Path of least resistance. — On the whole, therefore, it is fairly certain that the transpiration stream traverses the xylem strands, and that it is the lumina of the tracheae that form the chief conduits for the water. That some travels in the walls is quite probable, especially when the tracheae are partly blocked, as they often are, by gas, the path of least resistance being followed here as always. Nor is it impossible that some water moves in the cortex; but this is never enough to cover any considerable loss by evaporation.

Ascent of water. — As to the forces concerned in the ascent of water, little that is definite can be said, for the problem is one of extraordinary complexity, and knowledge of the exact physical conditions is very difficult to attain. Nor is it likely that the problem could be solved were all the factors in the plant body known, simply for lack of knowledge of the physical principles involved.

Capillarity. — Some "causes" frequently assigned and popularly current may be definitely discarded. The first of these is capillarity, as commonly understood. The xylem ducts are narrow tubes. Water rises in capillary glass tubes above the level outside, and the smaller the bore the higher it rises. Oil rises in a twisted lamp wick by capillarity. What more simple than to "explain" the rise of water in the ducts of the xylem strands by ascribing it to capillarity, since here are "strands" and "tubes"? But surface tension (which is a better name for capillarity) implies a free surface, and within the duct there can be no free surface which is lifting, as in an open glass tube. If one appeals to the surfaces bounding the bubbles of gas so common in tracheae (see p. 350), it must be remembered that for every meniscus concave upwards there is one concave downwards to balance it. Nor can one neglect the numerous transverse walls in the xylem of angiosperms,[1] and the fact that all the effective xylem of gymnosperms is composed of tracheids. How surface tension forces may operate at the evaporating surfaces in the leaves is not known; but these are not the ones referred to when capillarity is invoked as the cause of the ascent of water, or at least an aid to it.

Root pressure. — Root pressure (see p. 336) is frequently alleged to be active in forcing water up; and it is even held to be adequate in the case of the herbaceous plants and low shrubs, though confessed to be insufficient in the taller trees. The radical difficulty with turgor in the root cortex as a cause of the ascent of water, or at least an aid to it, is that it does not exist when it is most needed. In the very nature of the case the root cortex can be fully turgid only when it has an abundance of water; and it is not likely to have that when evaporation is active. To develop root pressure it is necessary to check evaporation, as by decapitation, and only *after a time* does water begin to ooze from the xylem in consequence of turgor. Often water at first enters the stump of a decapitated plant, showing clearly that there was no surplus of water under previous

[1] The longest continuous ducts found exceed 5 m., but those 1 m. long are rare, and the average is probably less than 10 cm.

conditions. Nor can root pressure be invoked even as an aid. For unless maximum turgor can be attained no extrusion of water from cortical cells is possible.

If a boy could push a wagon while the horse walked, he would be unable to push as soon as the horse's speed exceeded his own. If he clung to the wagon, he would be merely a drag, though if he ran he would be less of a drag than if he made no exertion. The transpiration horse often goes too fast with the water wagon for the root pressure boy to push. Then his grip is broken at once and he is no drag on the load, for root pressure cannot even hold on like the boy and "help" by not being wholly a drag.

Atmospheric pressure. — Atmospheric pressure has been invoked as an explanation. It is found that the gases which develop in the tracheae are often under a pressure less than one atmosphere. Indeed they develop there readily because this is the case. The tracheae, it must be remembered, are dead cells; their lumina therefore are as free to be occupied by gases as are intercellular spaces. Whenever the concentration of gases dissolved in a free liquid exceeds the amount normal at one atmosphere pressure, the gas particles escape from solution and form bubbles.

This happens when any bottle of liquid "charged" with CO_2 is opened. The gas is dissolved in the liquid under a pressure greater than one atmosphere; on uncorking it the pressure is reduced immediately to that of the outer air, the gas flashes at once into bubbles, and portions of the liquid are often forced out of the bottle by the violence of effervescence.

Bubbles would inevitably form in the water of the tracheae, whenever that water has the pressure on it reduced below one atmosphere. If this pressure were equal to half an atmosphere, it is argued that such tension could "lift" water about 5 m. So it could, if the lower end of the water columns were open to the pressure of the atmosphere and there were no resistance. If one took away half an atmosphere of pressure from the upper end of a water column and left a whole atmosphere of pressure to act on the lower end, of course the water would rise to the point of equilibrium. But these conditions do not exist in the plant. Evaporation may reduce the pressure on the water in the tracheae, but the lower end of the water column is not open. The living cells of the root cortex are interposed, and water cannot be driven through them by a difference of half an atmosphere or even a whole atmosphere of pressure; nor has the pressure in the tracheae ever been found to fall to zero. If it *were* zero, and there were *no resistance* to the movement, water could be pressed up to a height of only 10 m., a small fraction of the 100 m

which the tallest trees attain. Atmospheric pressure therefore is utterly inadequate at best. The most that can be allowed is this: by how much the difference in atmospheric pressure in the tracheae and in the air tends to make it easier for water to pass through the root hair and the root cortex, by so much atmospheric pressure may be said to help in the entry of water. But the very fact that these differences exist shows that they are not compensated by the movement of the water. In fact the difference between inner and outer pressure seems to be rather a result than a cause of water movement.

Role of living cells. — The ultimate cause of the ascent of sap is transpiration; but how it acts is entirely unknown. The energy employed in vaporizing the water is adequate to lift it miles high; but how is it applied so as to keep a continuous stream rising?

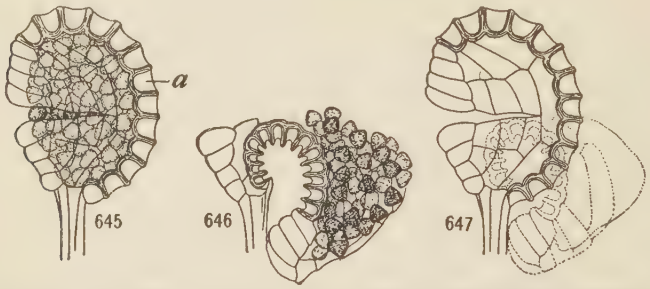
One link in the chain is the osmotic relations of the living cells of the leaf; for if the leaves be killed, evaporation continues from their cells, but the supply from the xylem strands is interrupted and the leaf dries up promptly.

It was also proposed, first many years ago, to ascribe the ascent of water to the action of living cells along the course of the xylem strands, and this theory is being advocated again to-day. One notion of their action was that it is like that of relay pumps, which take water in at one level and force it up to a higher level. It is difficult to conceive the physics of such an operation, and there is no anatomical evidence of such a mechanism, unless the cells of the pith rays are the active cells. The experimental evidence as to the cooperation of live cells in the process is contradictory, to say the least, and by its very nature the theory must be rather vague. That the living cortex and wood parenchyma are necessary to keep the xylem in proper condition for conduction is assumed.

Cohesion theory. — A current theory, which also is confronted by many difficulties and leaves much to be explained, is based upon the fact of the cohesion of water. That seems, at first blush, like talking of the strength of a rope of sand; but it is actually very difficult to break a small column of water, if sidewise or shearing strains are eliminated. The cohesive strength of water is variously estimated by physicists at 10–150 atmospheres.

The rupture of sporangia of ferns and the anthers of flowering plants, and the collapse of cells on drying, have now been shown to depend upon the cohesion of water. The mechanism for spore scattering in the sporangium of a fern, for example, is illuminating. It consists of thick-walled cells around the edge, the annulus

(*a*, figs. 645–647), which contain water. As the water evaporates it pulls the cell walls together, and in doing so straightens the ring and tears open the weak side. The thick elastic ⊂-shaped walls of the cells resist this compression, until finally the cohesion of water in the wall with the free water in the lumen is overcome, and the sudden elastic recoil of the annulus hurls the spores as from a sling.



FIGS. 645–647. — Rupture of sporangium of a fern (*Polystichum acrostichoides*): 645, the sporangium cracked; *a*, the annulus; 646, position of complete reversion, many of the spores adherent to the upper part of the sporangium; 647, position after recoil, the sporangium emptied; dotted lines in this figure show the position as in 646. — After ATKINSON.

This cohesion is predicated of the columns of water which occupy the tracheids and tracheae of the xylem, and it is coherent even through the end and side partitions (see theory of relation of water and cell wall, p. 301). If now any adequate lifting force could be applied at the upper end, the cohesion of the water is sufficient to enable it to hold together even to the roots of the tallest trees. That lifting force is evaporation, and the osmotic relations of water in the live cells of the leaf furnish the connection. Why the water columns do not break wherever bubbles of gas appear (and they must appear whenever the column is under any considerable strain), is not satisfactorily explained; and other like difficulties appear. Yet this theory at least faces in the right direction, seeking to give an account of the rise of water in purely physical terms. However, as this phenomenon has baffled investigators for more than a century, it may be a long while before it can be satisfactorily described.

4. OTHER LOSSES

Gases from the shoot. — Quite apart from the liquids and water vapor which escape from the aerial parts, there are gases which are constantly set free and leave the plant as such. These are carbon dioxid and oxygen; the former is one of the usual end products of respiration, and

the latter is a by-product of food making, but is used by all live parts in respiration. Carbon dioxid is continually produced in all live parts; but in green parts, when adequately lighted, it can be used for making food, and therefore in these parts under such conditions it never accumulates to an amount which permits it to diffuse out. Oxygen is only intermittently produced. When the green parts are making certain foods, its production is a measure of their activity; but that takes place only in the light. Since, therefore, the leaves are the green parts *par excellence*, oxygen escapes chiefly from them, because the amount produced is in excess of that used in their respiration. When it has accumulated in the cell sap to a concentration whose osmotic pressure is greater than its pressure in the air (*i.e.* about 0.2 of an atmosphere, or 152 mm. of mercury), it will fly off as a gas from the surface of the cell into the internal atmosphere of the aerating system. Likewise when carbon dioxid has accumulated to a suitable pressure (less than 0.0003 A., or about 0.22 mm. Hg.), it begins to diffuse into the air.

Diffusion from the root. — Oxygen can be formed only in green parts and hence escapes only from aerial parts; carbon dioxid, being formed in all live cells, can also escape through the other permeable region, the root. Its escape there may be directly into the soil water, whenever it has accumulated to a greater pressure in the cell sap. To demonstrate diffusion it is only necessary to grow the roots in contact with a polished marble plate (calcium carbonate), whose surface will be etched along the lines of contact because water, " carbonated " by the CO_2 escaping from the roots, converts the calcium carbonate ($CaCO_3$) into calcium bicarbonate [$Ca(HCO_3)_2$], which is readily soluble. Or by growing seedlings in water with phenolphthalein (an indicator which is rose red in weak alkaline and colorless in acid solution), the water will be decolorized by the roots; but the color will return upon boiling, thus driving off the CO_2 which had united with the indicator. Were any mineral or organic acids the cause of the decoloration, the color would not return.

But besides CO_2 other substances may leave the plant by way of the roots. At present these are not accurately known. Water cultures made with soil extracts indicate that organic compounds, often very deleterious to the culture plants, are frequently present. These may have come into the soil by diffusion from roots (see p. 315). Acid salts, such as hydrogen potassium phosphate, are probably not among the exudates, as once they were believed to be. Yet any substance in the root cortex, to which the cells are permeable, may escape; and when the matter is studied further, many compounds, now unsuspected, may be found diffusing into the soil water.

Mechanical losses.—Mechanical losses must also be taken into account. In all plants the drying of leaves, flower parts, rootlets, and even larger parts of the body, is followed sooner or later by their falling off. In annuals, the whole body perishes at the end of the growing season; hence the perennials offer the best examples. In woody perennials, particularly, the partial fall of the leaves in summer, due to heat, drought, or other causes, and the complete autumnal fall, are striking losses of material. Yet this is not so expensive to the plant as it might seem at first sight, for a large part of the available foods have been transferred from the leaves before their fall, and what is left is chiefly cell-wall stuff, unavailable organic matter, and ash. Nevertheless, much of that represents past expenditure of energy and is a dead loss; though by decay some of the materials again become available for rebuilding.

Fall of leaves.—The once active food-making machines go to the scrap heap in autumn and have no value except as junk. Their deterioration is progressive. In the leaves of woody plants as compared with other parts, there is with age, as a rule, a steady accumulation of dry matter and a rising proportion of ash.

Thus in the leaves of the European beech (*Fagus sylvatica*):

	May	June	July	Aug.	Sept.	Oct.	Nov.
Per cent dry matter . .	23.35	40.21	43.64	50.74	47.42	40.37	45.55
Per cent of ash . . .	4.67	5.20	7.45	9.03	8.90	10.80	11.42

In black locust (*Robinia Pseudacacia*):

	May	July	Sept.	Oct.
Per cent dry matter	26.50	35.90	44.30	44.60
Per cent of ash	6.25	7.75	8.22	11.74

In 500 leaves of the plane tree (*Platanus orientalis*):

	June	July	Aug.	Sept.	Oct.
Grams dry matter . . .	142.53	184.70	182.80	193.85	196.24
Grams of ash	8.70	14.62	17.81	20.12	21.33

Contrast with these figures the average ash content of the wood of such trees, which is about 0.7 per cent, with a minimum of 0.2 per cent and an occasional maximum of about 3 per cent.

This high ash content of leaves is not due merely to the retention of mineral matters when the water evaporated, as lime scale accumulates in a tea kettle.[1] Rather the using of certain constituents of the salts, particularly the nitrogen, sulfur, and phosphorus, left behind the bases, calcium, magnesium, etc., ready to enter into new combinations and to

[1] This is further evidenced by the fact that the ribs of leaves are usually richer in ash than the mesophyll.

reappear in the ash, when the organic matter is burned away, as CaO, MgO, etc. Moreover, certain mineral salts may be stored in the walls, as silica often is; and these reappear as oxids in the ash.

Fall of branches. — In woody perennials the competition between branches is so severe that many more die than survive. Thousands of rudimentary branches (as buds) never develop at all, and other thousands, after growing for a year or two, are outstripped by their more fortunately situated fellows, die, and drop off. The mortality is vastly greater than is realized without close observation, such as was made on a volunteer black cherry, and described in figurative language thus:

> The first year it made a straight shoot nineteen inches high, which produced twenty-seven buds. It also sent out a branch eight inches long which bore twelve buds. The little tree had, therefore, enlisted thirty-nine soldiers for the coming conflict. The second year twenty of these buds did not grow. Nineteen of them made an effort, and these produced three hundred and seventy buds. In two years it made an effort, therefore, at four hundred and nine branches, but at the close of the second year there were only twenty-seven branches upon the tree. At the close of the third year the little tree should have produced about thirty-five hundred buds or branch germs. It was next observed in July of its fourth year, when it stood just eight feet high; instead of having between three and four thousand branches, it bore a total of two hundred and ninety-seven, and most of them were only weak spurs from one to three inches long. It was plain that not more than twenty, at the outside, of even this small number could long persist. The main stem or trunk bore forty-three branches, of which only eleven had much life in them, and even some of this number showed signs of weakness. In other words, in my little cherry tree, standing alone and having things all its own way, only one bud out of every hundred and seventy-five succeeded in making even a fair start towards a permanent branch. And this struggle must have proceeded with greater severity as the top became more complex, had I not put an end to its travail with the axe! — BAILEY: *Survival of the unlike*, p. 88.

Loss of bark. — The constant flaking-off of bark, when the warping due to wetting and drying loosens the outer portions, or the steady weathering of the solid bark, occasions further losses of a relatively inexpensive kind. As in some cases waste products accumulate in the bark, this may be accounted one way by which the plant gets rid of wastes. Bark also contains a very large percentage of ash.

Fruits and seeds. — Fruits and seeds are separated annually from the body. These are loaded with surplus food for the embryo, and so constitute a most expensive loss — one that not infrequently distinctly impairs the vitality of the plant. The intermittent bearing of orchard trees, vines, etc., may herein find a partial explanation.

CHAPTER III — NUTRITION

1. THE NATURE OF PLANT FOOD

Food in general is organic. — The question, what is food for plants, elicits very different answers according to the point of view. The term *food* is not one which admits of accurate definition, and the difficulty increases the wider the range of organisms to which it refers. A lion obviously lives upon flesh, and the general constituents of his food can be determined. A sheep feeds on herbage, and that can be analyzed. A man consumes meat and vegetables of the most varied sorts. A fungus like *Penicillium*, which will grow on a glass of jelly or an orange or a piece of cheese or a plate of gelatin, obviously feeds upon vegetable or animal substances indifferently. The nutritive constituents of flesh and vegetables are many and diverse; plainly the term which is to include them must be most general. That term by common consent is *food*. It represents the totality of substances which nourish an organism and enable it to pass successively through the phases of its normal development. Now all the substances referred to belong to a category known as *organic*, because they are all produced by the chemical processes in a living organism. Food, therefore, for the lion, the sheep, the man, the mold, is composed of organic substances. It is true that there are also, in the very organic substances themselves and dissolved in the juices which make part of them, mineral salts of various kinds, and that these are indispensable to living beings; but their amount is very small indeed, and alone they are quite incapable of sustaining life. For the present, therefore, they may be left out of account.

Is the food of green plants inorganic? — The beings enumerated represent all sorts of organisms except the green plant. When we ask, "On what does the green plant feed?" the answer, based on analogy, has been, "On the substances that enter it — water, mineral salts, and carbon dioxid; for with these alone it can develop from embryo to maturity." These are inorganic substances; and if the answer be true, the food of green plants is inorganic and that of all other beings organic.

Is "food" food only for certain cells? — The first thing that awakens suspicion as to the wisdom of this answer is that the living matter of green plants is like that of all other living things, and it would be very strange if in them protoplasm could be nourished with inorganic substances, when in all others it requires organic material. Yet the green plant *might* be differently constituted; and it is said by way of explanation that this peculiarity is due to the presence of the green pigment, chlorophyll. On examining this point, it is found that only a part of the plant has chlorophyll. Most roots entirely lack it; only the outer cells of the stem ever contain it; and there are many cells, even in a thin leaf, and a great mass of them in a fleshy leaf, which are not green. Then we are forced to state the matter thus: the green parts of green plants use inorganic "food"; the colorless parts require organic food, for it is conceded on all hands that the colorless cells are unable to utilize any carbon dioxid and water. Whence it would seem that one cell might nourish itself with inorganic "food" and its next neighbor be unable to do so. That would certainly be a confusing situation if it could not be better described.

Is "food" food only at certain times? — It appears, further, that carbon dioxid and water can be "foods" only part of the time; namely, when the green cells are adequately lighted. So except in the day, even the green cell would require organic food! The situation would have to be stated thus: The "food" of the green cells only, and only by day, consists of carbon dioxid and water; the rest of the plant all the time and the whole of the plant at night must have organic food like all other living things.

Antithesis avoidable. — A little consideration shows that the apparent antithesis between green plants and other creatures is of our own making; it is produced solely by the application of the term *food* to the substances which enter the body, irrespective of their rôle. This antithesis can be avoided, and the confusion and contradiction eliminated, merely by avoiding this inept use of the term *food* and by applying it to organic substances only. By this expedient we escape a different use of the same terms in plant and animal physiology, with its resultant confusion of ideas, and we bring the green plants into line with all other beings, so far as nutrition is concerned. Excluding the inorganic substances from the category of foods, we need to recognize that one power possessed by green plants is unique: they alone make their own food, and not their own only, but food for the whole world. What they use for this food making — carbon dioxid and water — may be distinguished as food ma-

terials. What they make is universally known as food for their colorless cells, for non-green plants, and for animals. Why should it not also be recognized as their own food?

Food for plants is organic. — Food for plants, then, is like food for animals, always organic, the product of living beings; and in the last analysis, all food is made by green plants, for they alone among living beings have the power of making it out of the simple compounds CO_2 and H_2O.[1] They make it only in the green cells by the aid of light; and they make so much that they feed not only themselves, but all other creatures. The lion may live exclusively on flesh, but the flesh was built up by the herbivorous animal from the herbage it grazed, and the herbage was nourished by the foods it could itself make in sunlight. Man grows plants and appropriates the leaves, the roots, the stems, the fruits, or the seeds, improved by his selection and loaded with surplus food, for his own nourishment; or he feeds the steer, the sheep, and the hog with grass or grain that he may later use their flesh for his food.

What are the plant foods? — Having established a general meaning for the word *food*, the next question is: To what specific substances is it to be applied? Foods come from many sources and are of many kinds; and because they are so various, only the principal classes can be named, and a few examples briefly described. The four most important sorts are carbohydrates, fats, amides, and proteins.

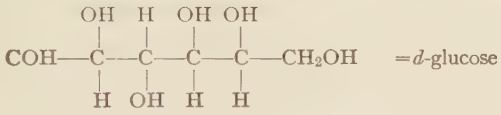
Carbohydrates. — Some carbohydrates are directly made by green plants; but there are also many that are secondary products. The name is no longer used in chemical classification; it is rather convenient than exact, just as "cryptogam" among plants or "invertebrate" among animals. Here belong the sugars, the starches, and the celluloses, each probably comprehending an indefinite number of different individuals. This is certain among the simpler sugars, whose composition is known; but only hypothetical for starch and cellulose, whose complexity has hitherto baffled all analysis.

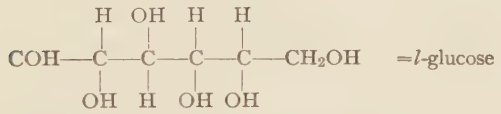
All these substances have a composition like this: $C_nH_{2n}O_n$, or $C_nH_{2(n-1)}O_{(n-1)}$, or $C_nH_{2(n-2)}O_{(n-2)}$, in which the value of n is 6 or a multiple of 6 where known, but may run up to several hundred. Thus grape sugar and its allied hexoses all contain $C_6H_{12}O_6$; while cane sugar and its allies consist of $C_{12}H_{22}O_{11}$. Starch and cellulose can be represented only as $n(C_6H_{10}O_5)$, with the value of n quite uncertain, but large. These empirical formulas, however, cannot convey any idea of the

[1] Certain bacteria also seem to be able to utilize these substances to form foods; but so far as is known the product is utterly trivial in amount, and the fact is entirely without significance, were it not for its exceptional character.

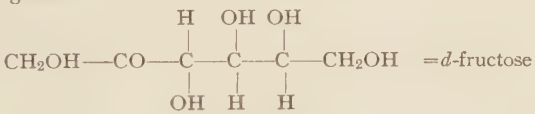
complexity of even the simplest carbohydrates, nor of the fact that a mere difference in the position of certain atoms or groups of atoms, which does not affect the percentage composition at all, gives wholly different chemical and physical characters to the substance.

Thus, grape sugar (glucose) exists in two forms, one of which rotates a beam of polarized light to the right and the other to the left; the one, *d*-glucose, is abundant in plants; the other, *l*-glucose, does not occur in nature but has been made artificially. The difference is shown partly in the three following structural formulas, which all sum up $C_6H_{12}O_6$:

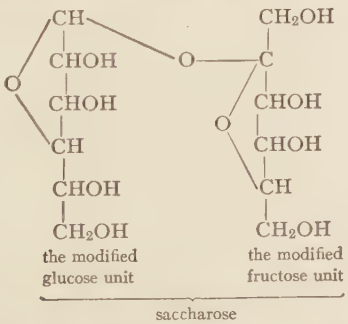




Further, fruit sugar (*d*-fructose) is abundant in plants, and its structure is quite different from glucose:



Another sugar especially abundant in plants, cane sugar, $C_{12}H_{22}O_{11}$, probably has this formula:

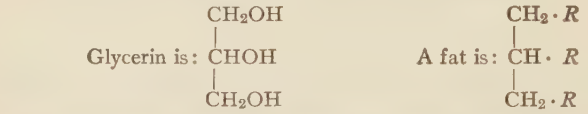


and when it breaks at the —O— bond, it takes up H·OH and resolves itself into a molecule of glucose and a molecule of fructose. These two hexose sugars, glucose and fructose, and the disaccharide, cane sugar, are the only sugars which occur in abundance in plants; though mannose, galactose, and maltose are formed in the course of digestion.

The simplest carbohydrate which has been detected in plants is formaldehyde, HCOH. This group will be recognized in the makeup of all the more complex ones above (but see p. 375). While it has only a transient existence and does not occur free, except in minute amounts, it has its special significance in that it is probably the first substance formed by the green cells from water and carbon dioxid.

Fats. — Fats are apparently always secondary products, and constitute a common form of surplus food. These storage products furnish various commercial oils; *e.g.* olive oil, cotton oil, linseed oil, castor oil, corn oil, etc. They occur usually in fluid form as minute droplets in the protoplast, only occasionally being solid at ordinary temperatures, as in the seed of cacao. They are of very complex structure, being compounds of glycerin and three molecules of fatty acid.

Their structure may be understood from these formulas:



in which *R* may represent oleic acid ($C_{18}H_{34}O_2$), linoleic acid ($C_{18}H_{32}O_2$), hypogaeic acid ($C_{16}H_{30}O_2$), or any other member of a considerable series of fatty acids, minus the acid ion H. The *R* radicals may be all alike or different. When digested, fats break up into glycerin and the fatty acid or acids. The fats contain a notably small proportion of oxygen.

The *lecithins* are substances allied to the fats in their constitution, containing phosphoric acid and cholin in place of one of the fatty acid radicals, *R*. They are very widely distributed in plants, and probably play an important rôle in the protoplasm, but just what is not known at present. It may be that they determine what substances may pass through the membranes; and it may be also that they are connected with the formation of chlorophyll.

Amides. — The name is here used loosely and not in its strict chemical sense, for a group of substances of which none are popularly known. For convenience, they may be distinguished as nitrogenous compounds intermediate between carbohydrates and proteins. On the one hand, they are derivatives of proteins, among whose decomposition products various amino-acids always figure. On the other hand, they are derivatives of the carbohydrates and their allies, from which, with proper additions, they are readily formed. In addition to the carbon, hydrogen, and oxygen of carbohydrates, they contain nitrogen, always combined

with hydrogen as a definite radical, NH_2, known as the amide radical. It may replace an H or OH group in the various carbohydrates and their allied acids, converting them by this slight change into quite different substances.

Thus, either acetic acid, $CH_3—COOH$, or glycolic acid, $CH_2OH—COOH$, becomes amido-acetic acid (glycin), $CH_2(NH_2)—COOH$, by the substitution of the amide radical NH_2 for hydrogen (H) or hydroxyl (OH), respectively. Glucose, $COH—CHOH—CHOH—CHOH—CHOH—CH_2OH$, becomes glucosamin $COH—CH(NH_2)—CHOH—CHOH—CHOH—CH_2OH$, by a like substitution. On the other hand, some of the constant decomposition products of the more complex proteins are glycin (*ante*); leucin, $\begin{matrix}CH_3\\CH_3\end{matrix}\!\!>\!CH—CH_2—CH(NH_2)—COOH$; tyrosin, $OH—C_6H_4—CH_2—CH(NH_2)—COOH$; asparagin, $CO(NH_2)—CH(NH_2)—CH_2—COOH$; in all of which the amide radical has replaced H or OH of an allied substance.

Proteins. — Proteins are the substances which compose the larger part of the cytoplasm; protein foods, therefore, are those which can be most directly used for nourishment, and so represent the end of food making. To define proteins is quite impossible; they are so numerous and so varied that scarcely any characteristic is universal. Within this huge group are included some substances which are relatively simple, and others whose complexity defies all analysis. Even the simplest are scarcely known chemically, the actual knowledge permitting only theories of their construction. It has been possible in most cases to determine only the percentage composition, which with a study of the decomposition products sometimes permits the establishment of an empirical formula. The more complex proteins contain sulfur, and some have also phosphorus in addition to the carbon, hydrogen, oxygen, and nitrogen of amides, with traces of ash, which may or may not be structurally a part of the protein. One nearly pure protein is familiarly known, the albumin or "white" of eggs; perhaps the best known plant protein is the one longest known, the gluten of wheat grains.

To illustrate the complexity of these substances and, as well, the uncertainty regarding their composition, the following formulas, though hardly more than guesses, are quoted. A crystalline vitellin from squash: $C_{292}H_{481}N_{90}O_{83}S_2$. An albumin: $C_{720}H_{1134}N_{218}O_{248}S_5$. Hemoglobin (of the blood): $C_{712}H_{1130}N_{214}O_{245}FeS_2$; the same, another guess, $C_{600}H_{960}N_{154}O_{179}FeS_3$.

The most familiar physical characteristic of many proteins is that they coagulate; heat, prolonged shaking, the action of acids, alcohol, salts, etc., cause the protein to change from a liquid or semi-liquid form to a firmer "clot," which by pressure can be separated into a fluid and a more solid portion. The coagulation of white of egg by heat, of milk on souring, and of the fibrin of blood on contact with a vessel are familiar examples. Ordinarily the coagulum is insoluble in water. But the neutral salts act differently, producing a soluble clot. Advantage is taken of this fact to separate various mixed proteins and purify them partially for analysis by "salting out." Other physical peculiarities are their high resistance to the electric current, their large molecular weight (probably 15,000 and more in many cases) and hence slow diffusibility, so slow usually as to be negligible.

Some proteins crystallize, but most do not. When first discovered such crystals were called "crystalloids," because it was not believed that true crystals could be formed by organic matter. They are regularly present in the protein grains of the Brazil nut, castor bean, etc. (fig. 664).

Plant foods again. — Plant foods, then, are specifically these complex organic compounds — not the simple inorganic substances out of which green plants alone can make food. This is practically implied in the terms proposed by authors who reject this use of the term food, and used frequently to distinguish plants as to their mode of nutrition, viz. *autotrophic*, or self-nourishing, plants, and *heterotrophic* plants. The obvious objection to these two terms, if they are anything more than convenient and figurative ones, is that only some parts of most so-called autotrophic plants are strictly self-nourishing. Only the plants whose every cell contains chlorophyll are actually autotrophic. If the term be used in the wide sense, green plants are not merely self-nourishing — they nourish all living things.

Kinds of food needed. — However, there is a wide difference among plants as to the kind of food that they require. The known variety is so great that it is impracticable to state it in detail here, and only a small number of plants, chiefly fungi, have been carefully studied in this respect. Some thrive best on comparatively simple compounds; others require the most complex proteins. Some flourish on material which is useless or even highly injurious to others. The proverb "what is one man's meat is another man's poison," is quite applicable to plants. Among the lowest and simplest plants, the bacteria, there are some which live upon substances almost as simple as the food materials of higher

plants; but they manage to secure energy in ways unknown to us, and build these substances into their bodies.

Food a source of energy. — After all, foods are of value to plants, as we conceive things, because they supply them with energy as well as with material. The energy income in this way is indeed the important feature. The green plant locks up in the food it constructs a fraction of the solar energy which reached it as light; and thus this energy becomes available to other organisms, since after further transformations of the foods they can release it by decomposition and apply it to other reactions.

Food and growth. — Because with our best appliances we are unable to know yet the real nature of nutrition, the use which a plant makes of food can be determined only by the extent to which it promotes growth and development of the body. The term *economic coefficient* has been used to express the ratio which the increase in the weight of a crop (say of a fungus) bears to a given quantity of a particular food. Manifestly there are other ways in which the plant uses a food besides incorporating it into the permanent structure of the body, and many complicated relations may be disturbed by too limited nutrition. Yet this economic coefficient expresses, in a crude way, the differences in the availability of foods for body building, and so impresses the fact that the processes of nutrition differ widely in different plants.

2. PHOTOSYNTHESIS

The fundamental fact in the nutrition of all living things is the capacity of green plants to make certain complex organic compounds, carbohydrates namely, out of carbon dioxid and water, by the aid of light. This unique process is known as *photosynthesis*.

The term used. — When the food of green plants was described as inorganic, this transformation of inorganic materials into carbohydrates, which was taken to be their incorporation into the body, was called assimilation, after the analogy of the transformations undergone by the food of animals. As the radical differences between the food making of a green plant and true assimilation in both plants and animals began to appear, an attempt was made to obviate the confusion by using the term *carbon assimilation*. These terms are still in common use in other countries, but will gradually disappear.[1] Clearness demands the use of the dis-

[1] For example, a recent hybrid is "photosynthetic carbon-assimilation"!

tinctive term *photosynthesis* for the process that is peculiar to green plants, leaving the term *assimilation* to be applied to the same process in both plants and animals; namely, to the transformation of foods of all kinds into the actual living stuff.

As photosynthesis requires a supply of certain substances, which reappear in more elaborate form, and acts through certain structures, which require a supply of energy for doing the work, the making of carbohydrates may be described appropriately in terms of a manufacturing process. There are (1) the raw materials, (2) the laboratories, (3) the energy, (4) the products and the process.

(1) The Raw Materials

Carbon dioxid. — The raw materials needed have already been named, carbon dioxid and water. Carbon dioxid exists everywhere in the air, in the ratio of about 3 parts in 10,000, and its nearly uniform distribution is assured by the convection currents (winds) that stir the atmosphere. Only in the neighborhood of cities or other places where CO_2 is being produced in quantity is there temporarily an excess. By decomposition of rocks, burning of fuel, decay of organic matter, and respiration of plants and animals, the supply of CO_2 is maintained, though great quantities are removed from the air by green plants. The amount is constant, so far as can be known historically, though there is geological evidence that in earlier periods of the earth's development CO_2 existed in much larger and also in smaller quantities than now, since enormous amounts have been fixed in beds of limestone, and later released by weathering.

CO_2 near the ground. — On quiet days there is a layer of air near the ground where the proportion may rise much higher (10 to 12 times as much), owing to the diffusion of CO_2 from the soil, where it is being evolved by the decomposition of organic matter through the agency of bacteria, etc. Perhaps turf-forming and rosette plants profit from the lowly position of their leaves, since the more CO_2 in the air, within limits, the more can enter them and be used for food making.

CO_2 in water. — In the water of quiet pools and lakes, as well as in slow streams, the amount of CO_2 dissolved is much greater than in the air. It is produced by the host of organisms living in the waters and by decay, and is also dissolved from the air. As CO_2 is very soluble in water (up to volume for volume at ordinary temperatures), it may

thus accumulate to 25 or even 100 times as much as in the air. This puts water plants in a very advantageous position so far as a supply of CO_2 is concerned.

Admission of CO_2. — Of course in all plants that present an uncutinized (and consequently a wet) surface to the air, the CO_2 enters directly at the surface; in fact it can enter, in proportion, wherever water can evaporate. As the cuticular evaporation in most of the higher plants is small, the quantity of CO_2 entering through the epidermis is trifling. Into some epiphytic seed plants which have no stomata (*e.g. Tillandsia*), the leaves of mosses, the thallus of liverworts, etc., CO_2 enters directly.

The supply for the great majority of the larger land plants, however, passes through the stomata. These openings are ample to admit not only what is necessary, but five or six times more than actually passes through them in nature.

It has been shown that CO_2 will diffuse through a multiperforate partition, placed over some ready solvent like sodium hydroxid, as freely as it would enter the solvent were the partition absent, provided the perforations are not farther apart than ten times their diameter. The epidermis is like such a multiperforate partition in which the area of the openings is scarcely more than 1 per cent of the total surface. But the CO_2 dissolves so readily in the wet cell walls bounding the intercellular spaces that its pressure in the internal passages is usually 0; so it may traverse the stomata as rapidly as is permitted by the gradient of pressure, 0.228 mm. outside to 0 inside. The speed of the molecules is found to be greatly accelerated as they swirl through the narrow passage of a stoma; in fact, they traverse it at a speed about 50 times as great as when diffusing freely into sodium hydroxid.

Even when the orifice of the stoma is partly closed, though this reduces proportionally the amount of gas passing, the supply of CO_2 is not likely to fall below the maximum that can be used. As in good light the stomata are usually more than half opened, even though the evaporation is excessive, an adequate supply of CO_2 is thus assured, so far as admission to the aerating system is concerned.

Deficiency in CO_2. — As a matter of fact, however, the supply of CO_2 is often less than could be utilized by the chloroplasts. This is shown by the fact that photosynthesis is increased when, in good light, the amount of CO_2 in the air around the plant is artificially increased. The increase may go to a hundredfold or more with positive benefit, at least so far as brief experiments show. Any increase in the air means increased pressure of CO_2 in the aerating passages; and this means the solution of more CO_2 in the wet walls, and consequently faster diffusion

toward the chloroplasts, where the CO_2 is actually utilized. Here, indeed, is the point at which the normal pressure of CO_2 usually limits the process of photosynthesis. The main-line transportation through stomata and intercellular spaces is adequate, but the switching facilities in the terminal yards (from cell wall to chloroplast) are not; hence when otherwise capable of operating to full capacity, the laboratories are hindered by the impossibility of securing enough of this raw material. There are other factors which may limit the output, to be discussed later; but the shortage of CO_2 due to low diffusion pressure is the commonest.

Water. — Water, the other of the raw materials, is never lacking when plants are active. Its source for most land plants is the soil water that enters through the roots. The little that may enter *via* the leaves (comparable with the amount leaving in the same time by cuticular evaporation, p. 327) is practically negligible. Only in mosses, liverworts, and a few epiphytes, *i.e.* plants with practically uncutinized surfaces, may it freely enter aerial parts. In many such cases there are special structures that hold water until it can enter.

Relation of CO_2 and H_2O. — The carbon dioxid and water enter into a double relation. In part, the CO_2 is merely dissolved in the water; in part the two form a loose chemical combination, carbonic acid, H_2CO_3. This three-phase system, solute, solvent, compound, is in equilibrium, and if the amount of any member is altered, corresponding changes take place in others and equilibrium is again reached.

(2) The Laboratories

Chloroplasts. — The laboratories in which photosynthesis proceeds are the chloroplasts. These are organs of various form and size, found only in superficial parenchyma cells, *chlorenchyma*, of stems and foliage. (For a discussion of this tissue and its relations to external agents, see Part III, p. 530.) The chloroplasts are embedded in the cytoplasm just within the ectoplast and marked by their green color. In a few algae (especially the Conjugales, p. 37) they have various and sometimes fantastic forms, but in almost all the higher plants they are shaped like a bun or a thick round cake; that is, two diameters are nearly equal, and the other is shorter, with the convexity greater on one face than the other (see fig. 619, p. 297). Their form is subject to change from internal causes, and in moving about with the cytoplasm they are easily distorted

by pressure, showing that they are of a soft, elastic, and semi-fluid consistency.

Pigment and stroma. — In fact, the body or *stroma* of the chloroplasts seems to be like the cytoplasm, but dyed by the green pigment. The precise relation between the pigment and the stroma has not been satisfactorily made out, even in the killed chloroplast, and in the live unaltered chloroplasts it can only be conjectured. In some cases, when the pigment has been dissolved out by alcohol, the stroma (of course coagulated by the alcohol) presents a spongy appearance, and it has been inferred that the meshes of the sponge throughout were occupied by pigment. In others, especially in the larger chloroplasts which can be sectioned, the pigment seems to be restricted to a spongy shell of measurable thickness at the surface, while the interior is colorless.

Pigments. — The yellow-green pigment is called *chlorophyll;* but it is not a single substance. Several pigments can be separated more or less completely, of which only two are abundant and constant in all higher plants, the one bluish green and the other pale yellow. The names applied to these are confusing. To distinguish them we shall employ the terms *chlorophyllin* and *carotin*. To the bluish green one no distinctive term has been generally applied, but it has been usually called chlorophyll (not distinguishing it from the combination), or chlorophyll proper. For the yellowish one, *xanthophyll*, *etiolin*, and *carotin* have been used. The last is preferable.

The term xanthophyll is descriptive, but it has also been used for other minor yellow pigments. Etiolin was applied to the pale yellow pigment which appears when plants have been "etiolated" by being grown or kept for a time in darkness. It seems to be identical with the yellow pigment named from the carrot, carotin, which proves to be very widely distributed in plants.

Chlorophyllin and carotin may be partially separated by their unequal solubilities. If to a fresh solution of chlorophyll in 80 per cent alcohol, benzene be added, the mixture shaken, and then allowed to stand, the benzene rises, carrying the greater part of the chlorophyllin, while the alcohol retains the greater part of the carotin.

Chlorophyllin. — The chemical composition of chlorophyllin is not known. It is very easily altered and is certainly very complex, containing N as well as C, H, and O. Whether phosphorus or magnesium is an essential constituent is in contention. Iron does not seem to be an integral part of it, though considered essential to its formation. The red coloring matter of the blood, hemoglobin, yields decomposition prod-

ucts very like those of chlorophyllin, suggesting that the two pigments have structural similarities. That both have peculiar relations with carbon dioxid is interesting, but cannot yet be explained.

When chlorophyllin disappears in the autumn, the yellow pigments become prominent, and some of its decomposition products have a share in reddening the tissues. The red pigments are then dissolved in the cell sap; the yellows are still in the chloroplasts. The autumnal coloring, however, is not yet fully understood.

Carotin. — The chemical composition of carotin is certainly very different from that of chlorophyllin. Its formula, probably $C_{26}H_{38}$ or $C_{40}H_{56}$, shows that it lacks both O and N. It is widely distributed in plants, and to it chiefly the orange and yellow tints of flowers, fruits, seeds, roots, etc., are due.

(3) The Energy

Light. — While the intricate chemical relations of chlorophyll are yet unknown, one of its physical features is known to be of the greatest importance. That is its capacity to absorb radiant energy. When the radiant energy coming from the sun is passed through prisms of rock salt, glass, or other appropriate media, or is reflected from a minutely striate surface, the various wave lengths are unequally refracted or reflected, so that the physiological and other effects of energy of different wave lengths can be studied. Certain of these wave lengths (if they were sound waves one might say about 1 octave out of 11) affect our eyes, and this physiological effect is what we know as light. By a figure of speech the cause is likewise so named, and the waves themselves are called "light." But they differ only in length and frequency from the much greater number, both longer and shorter, slower and faster, which we cannot perceive with our eyes. Other physiological effects, such as inflammation of the skin and the development of pigment ("sunburn"), are produced by light waves. On the plant, likewise, waves of different lengths produce different effects according as certain parts are attuned to them (see p. 449).

Absorption spectrum. — The chlorophyll is so constituted that it can absorb waves of certain lengths, all falling within the range of our vision. On the plant this energy cannot produce the effect that it does on our eyes, and hence for the plant it is "light" only by a convenient figure of speech. There are seven separated groups of waves whose absorption is more or less complete. When we look at a spectrum of

sunlight, *i.e.* a narrow bar of light dispersed into a band of different wave lengths, each group of waves produces its appropriate effect and we see a band of blending colors, dark red at one end, running through red, orange, yellow, green, blue, indigo, violet, and ending in the darkest violet. On interposing a leaf in the path of the light, there appear across the spectrum dark strips due to the partial or complete stoppage of the energy. Similar *absorption bands*, slightly displaced, are seen by using in the same way an alcoholic solution of chlorophyll (fig. 648).

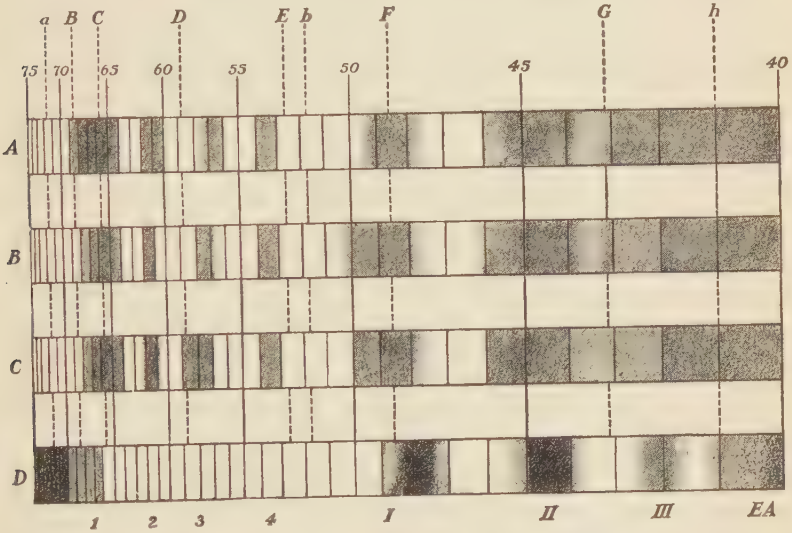


FIG. 648. — Absorption spectra: *A*, chlorophyll of *Allium ursinum* in alcohol; *B*, chlorophyll of English ivy (*Hedera Helix*) in alcohol; *C*, chlorophyll of *Oscillatoria* in alcohol; *D*, carotin. 1, 2, 3, 4, absorption bands of chlorophyllin; *I*, *II*, *III*, absorption bands of carotin; *EA*, end absorption. The lettered broken lines mark the position of the principal absorption lines of the solar spectrum (Fraunhofer lines); the numbered solid lines form a scale from which wave lengths (λ) in millionths of a millimeter may be found by adding a cipher; note the increasing dispersion from left (red) to right (violet). — After KOHL.

These absorption bands are as follows: 1, in the red a wide black one, its wave lengths (λ) being 670–635 $\mu\mu$[1]; 2, a narrower and less intense one in the orange, λ = 622–597 $\mu\mu$; 3, in the yellow, a band much lighter than 2, and shading out on the sides, λ = 587–565 $\mu\mu$; 4, a faint band in the green, not always to be seen, and probably due to decomposition products, λ = 544–530 $\mu\mu$. Ordinarily the other three blend into one, and there are no visible waves left beyond the blue (λ = 495–420). By very careful manipulation, using dilute solutions instead of a leaf, they can be distinguished, their limits not being sharply marked.

[1] The exact location of the bands varies. 1 $\mu\mu$ = 0.000001 mm.

The bands 1–3, and possibly 4, belong to chlorophyllin, while the indefinite three, *I–III*, belong to carotin. These three are much better seen in the absorption spectrum of carotin alone (fig. 648, *D*).

Fluorescence. — Chlorophyll has another physical character, which it shares with some other dyes; its solution is fluorescent. When a strong solution in alcohol is held between the eye and the light, the color is a vivid green; but if examined by bright reflected light, it appears deep blood-red. While this is a useful recognition mark, the physiological significance of fluorescence, if any, cannot be explained.

The absorbed energy. — The energy that drives the machinery is derived from light, for if a green plant be kept in darkness, it is entirely unable to make any carbohydrates. Furthermore, it is only the chloroplast directly illuminated that receives this energy. A lighted portion of a leaf cannot communicate the energy to a darkened area. If a portion of a leaf be covered with an opaque plate, while CO_2 is allowed free access, the rest of the leaf may show evidence of active photosynthesis, but the darkened area shows none. Moreover, it is the energy absorbed by the chlorophyll that does the work.

The following experiment shows this: A plant was kept in the dark until its leaves showed no trace of starch. Then on a sunny day a spectrum of sunlight, as bright as possible, was cast on a leaf and kept steadily in the same place for some hours. Thus the chlorophyll could absorb energy only in those regions along the band of light where fell the waves of lengths that it can stop; on the leaf these regions of course corresponded in position to the absorption bands before described. If, therefore, the leaf works with the absorbed energy, photosynthesis can occur only in these strips and not elsewhere. After the exposure, on testing the leaf for starch (the accumulation of which is a mark of active photosynthesis), it was found in abundance where lay absorption band 1 (fig. 648), and scantily in others; but it was wholly lacking in other parts of the spectrum.

This is what would be expected; but there was once an idea that chlorophyll acted merely as a screen, shading the protoplasm from harmful rays of light; and that the protoplasm could work properly only behind such a screen. There is now evidence that the protoplasm is unnecessary in the first stages of carbohydrate synthesis, those strictly called photosynthesis. It is probably light transformed to electricity that reduces the H_2CO_3 to formaldehyde (see p. 375), which then condenses into more complex carbohydrates.

Exposure to light. — Plainly the light which has passed through a chloroplast is unlike that which has not; and the more chloroplasts it passes through, the more complete is the absorption of effective waves. The upper cells of a leaf, therefore, are in a more favorable position with respect to light than the lower, especially in weak or diffuse light; but

if the stomata are only on the under surface, as they often are, the lower cells are more favorably placed with respect to CO_2; and the more so as the looser arrangement of these cells permits freer diffusion. The very structure of the leaf is in large measure a response to these different factors, and so perhaps the advantages and disadvantages balance one another. A leaf which is directly shaded by another is obviously in a decidedly disadvantageous situation; and we observe various arrangements and positions that reduce shading. These result in leaf mosaics of various kinds (see Part III, p. 543). A plant that grows in shade is different from the same species grown in the sun; indeed shade plants have peculiarities which depend in large part on the difference in the illumination (see Part III, p. 531).

Energy obtained. — An ordinary thin leaf reflects and absorbs 40–70 per cent of the sunlight which falls upon it; but of diffuse light it absorbs about 95 per cent. The chlorophyll itself seems to absorb something like 20–30 per cent, but of this only a small part can be used for photosynthesis and so stored as potential energy in the carbohydrate made. That amount is variously estimated from 0.5 to 3 per cent. The balance is free to heat the leaf, whose internal temperature in the sun sometimes rises 10–15° above that of the air. This surplus heat, of course, is partly transferred to the air adjacent, but the greater part becomes latent in the water, whose vaporization is accelerated thereby. This is the so-called "chlorovaporization" (see p. 330).

Deficiency in light. — It will be evident from the foregoing that in nature light is seldom lacking to drive the machinery rapidly enough to dispose of all available CO_2. Yet it may be reduced to an intensity at which light, instead of the small supply of CO_2, limits the output. For example, some plants are so situated that they get only 2 per cent of the total sunlight in the vicinity. From the point at which the effective energy of the light absorbed is just equal to disposing of the available CO_2, whether this is greater than natural or not, lessening the intensity of the light results in a proportional diminution of the amount of the product.

Efficiency. — It will be further evident that the plant is a very inefficient machine, considering the relation of energy received to the energy stored in the product. A steam engine which delivers as mechanical power less than 10 per cent of the energy of the fuel consumed under the boilers is fit for the scrap heap, and the best types are delivering above 15 per cent. Contrast this with the 0.5–3 per cent of the plant economy.

Yet in spite of this relative inefficiency, the total product is enormous and invaluable, because of the limitless store of energy pouring upon the earth constantly from the sun, beside which the artificially released energy of fuel is absolutely a negligible quantity.

The solar energy received by the earth in a *second* is represented by 250×10^{15} calories. The coal consumed in the whole world in a *year*, reported in 1906 as about 1000 million metric tons,[1] represents 8×10^{15} calories. The plant can afford, so to speak, to be inefficient.

Source of light. — The source of light is quite a matter of indifference. In nature, of course, the primary source, the sun, is alone to be considered, since the light of even the full moon (only $\frac{1}{600000}$ that of the sun) is too weak to effect photosynthesis to a measurable extent. Various secondary sources may be used in experiments, some electric lamps and the incandescent mantles (with gas) giving light of sufficient intensity when near the plants. Attempts to "force" plants, by enabling them to make food by night with electric arc illumination, have been successful with certain sorts, showing that there is no need for rest at night, and that a greater supply of food permits more rapid development; but there will be no incentive for commercial application of this result until the cost of electric energy is vastly less than now.

Temperature. — A suitable temperature has usually been considered merely a condition of photosynthesis, and not a source of energy for the process. This is evidence that our knowledge of the energy relations of this process is vague, and that the matter needs investigation. At present, however, it is not possible to describe in terms of energy the effect of heat upon photosynthesis, so we must be content with a brief statement on temperature as a condition.

Experiments show that even at temperatures approaching 0° C. some plants can make carbohydrates; the algae of arctic waters are conspicuous examples. Yet for most plants such a low temperature practically stops photosynthesis; while even at several degrees higher it may be the limiting factor, less food being made than the CO_2 and light would permit. Likewise in direct sunlight the temperature may rise so high in the interior of a leaf as to retard photosynthesis[2]; and in tropical deserts, where the heat of the air itself may run to 45° C., it is probable that photosynthesis is reduced thereby.

[1] The metric ton about equals the English "long" ton, 2200 lbs.

[2] But these heating effects of direct sun are compensated in a measure by evaporation

(4) The Products and the Process

The products. — The first product of photosynthesis is not known with entire certainty, and the process, therefore, cannot be described accurately. The product of later synthesis which is most general and has been longest known is starch. The fact that it is so generally present and that it is so universally used as evidence of photosynthesis because it can be so easily detected, tend to confirm the common impression that starch is *the* product of photosynthesis. But there are many plants in which starch is either not formed at all, or appears only under exceptional conditions, and in no plants is it the exclusive product. Thus, in most fungi no starch is formed when they are fed on carbohydrates; in the kelps fucosan takes its place, and in many monocotyledons, oil; while even in the plants which produce starch abundantly, much of the earlier product is diverted into amides and possibly other nitrogenous compounds.

In any event starch is a secondary product, and represents the surplus in the manufacture of primary carbohydrates over immediate use, removal, transformation into amides, etc. That starch does not appear under certain conditions, in a leaf in which it is usually formed, is no evidence, therefore, that no photosynthesis has occurred, but only that it has not gone on at a rate rapid enough to yield enough excess to appear as starch.

Amount of product. — A method of estimating the amount of photosynthesis under various conditions is based upon the relative weight of equal, but necessarily small, areas of leaves, taken at the beginning and end of the experimental time, allowances being made for migration [1] and use by data from other experiments. The results at best cannot be exact, and the introduction and multiplication of small initial errors make the calculations based on these data quite unreliable.[2]

When accurate data for photosynthesis are needed, the only reliable method is to determine the amount of CO_2 used. This requires rather complicated apparatus, skillful manipulation, and accurate gas analysis. This method is obviously independent of the products and their use or migration.

[1] Or this may be rendered impossible by severing the leaf from the plant.

[2] The results obtained by this method are two to three times as large as those in the table on the following page.

The best estimates as to the amount of photosynthesis carried on by thin-leaved plants are given in the following table:

CARBOHYDRATE MADE IN 1 HR. BY 1 SQ.M. OF LEAF SURFACE

NAME OF PLANT	CONDITION OF LEAF	LIGHT	TEMP. °C.	CO_2 USED, CC.	CO_2 USED, MG.	CARB. MADE, MG.
1. Helianthus annuus . .	attached	diffuse	21.1	312.6	612	392
2. Helianthus annuus . .	detached	diffuse	19.0	439.9	862	551
3. Helianthus annuus . .	detached	strong to diffuse	26.8	385.3	755	483
4. Helianthus annuus . .	attached	bright sun	47.1	21.9	43	27
5. Tropaeolum majus . .	detached	diffuse	21.7	158.3	310	198
6. Tropaeolum majus . .	detached	diffuse	25.9	243.7	487	305
7. Catalpa bignonioides .	detached	interm. sun	20.0	373.2	737	468
8. Petasites albus . . .	detached	interm. sun	17.0	208.4	408	261
9. Polygonum Weyrichii .	detached	. . . .	21.0	473.2	927	593
10. Prunus Laurocerasus .	detached	. . . .	10.0	. . .	. . .	281
11. Prunus Laurocerasus .	detached	. . . .	37.5	. . .	. . .	810
12. Helianthus annuus . .	detached	. . . .	19.0	. . .	. . .	569
13. Helianthus annuus . .	detached	. . . .	29.0	. . .	. . .	650
14. Helianthus annuus . .	detached	. . . .	35.0	. . .	. . .	730

Nos. 1–9, after BROWN and ESCOMBE, in part recalculated; nos. 10–14, after BLACKMAN and MATTHAEI, especially intended to show the effects of temperature on photosynthesis. An effect of excessive temperature is to be seen also in no. 4.

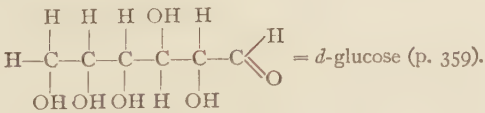
Using such results as the basis of calculation, it would be easy to show how enormous a weight of food is made in a growing season by the foliage of meadows and forests. But unknown allowances must be made for leaves unfavorably situated or lacking in vigor, and such estimates are of little value except for their impressiveness. The value and volume of the annual crops of cultivated plants is even more impressive; and to this must be added in imagination the unknown but huge volume of wild vegetation, all dependent upon photosynthesis for at least 85 per cent of its dry substance.

The following are the approximate values of some of the more important crops of 1909 in the United States: corn, $1,720,000,000; wheat, oats, rye, and barley, $1,280,000,000; cotton, $850,000,000; hay, $665,000,000; potatoes, $212,000,000. Together the weight of these marketable products is something like 175,000,000 metric tons; and of course this is but a small fraction of the vegetation that pro-

duced them. In addition to the staple crops just named, whose aggregate value in 1909 was about $3,000,000,000, other farm crops add nearly as much more, being estimated at $2,700,000,000. Such are the values that plants annually produce in this country, chiefly from the air and water, by photosynthesis.

Process. — The process of photosynthesis is not certainly known; but all the evidence points strongly in one direction; so that the hypothesis of von Baeyer may be considered as highly probable. It appears that the carbonic acid ($CO_2 + H_2O \rightleftarrows OH{\cdot}COOH$) is by some means reduced, perhaps first to formic acid ($H{\cdot}COOH$), and later to the simplest carbohydrate, formaldehyde ($H{\cdot}COH$). In the course of this reduction a molecule of oxygen, O_2, is set free and appears as a by-product.

The reduction of H_2CO_3 to formaldehyde has lately been accomplished artificially, though much less efficiently than in plants. A thin layer of chlorophyll on gelatin or floating on the surface of water (to which has been added an enzyme that will break up hydrogen peroxid, H_2O_2, into water and oxygen), when supplied with CO_2 in light permits the accumulation of formaldehyde and oxygen to a measurable extent in the apparatus. The formaldehyde molecule so quickly combines with others of its kind that it has been difficult to prove its formation in leaves. Free, it is a powerful poison, even in dilute solution (1 : 20,000); but its prompt condensation into some hexose sugar prevents accumulation to a harmful extent. The details are probably as follows: six molecules of formaldehyde, $H-C\langle^{H}_{O}$, unite into a chain. This union engages two of the four bonds of each C atom, except at the ends, where only one is concerned. This consequently either releases one of the two O bonds or leaves one H atom free, or does both. The free H immediately joins its neighboring half-free O, and together they form OH, bound to C by only one bond. At one end no H is freed; but the half-freed O takes up H and the group becomes CH_2OH, characteristic of an alcohol. At the other end, the loss of one H leaves the aldehyde group $C\langle^{H}_{O}$ as in formaldehyde. In glucose a further transposition occurs in group 4, H and OH exchanging places.



= *d*-glucose (p. 359).

Glucose and starch. — Glucose probably represents the first stable carbohydrate formed in most plants; yet there is some variation in this respect in different plants, and there is evidence that in some cases cane sugar, saccharose, is the chief product. It is quite possible, moreover

to divert some of the product into amides by a simple substitution of the amide radical, NH_2, for some H or OH radical. Thus, if the fifth group in the glucose chain became $HC(NH_2)$, the product would be glucosamin, a substance of quite different properties (see p. 360). Like diversion by substitution might readily occur if only two or three formaldehyde molecules had come together. Such processes seem to be the initial steps in protein synthesis (p. 380).

The common main product, glucose, usually accumulates in the cells because it is formed faster than it can move away. Finally starch or some other stable product appears. The intervening steps are hypothetical. It seems that at a certain concentration glucose molecules show a tendency to combine with each other to form a compound sugar, maltose ($C_{12}H_{22}O_{11}$), which promptly compounds itself in like manner into a dextrin and finally into starch. The combinations occur rapidly, and the intermediate products are hence obscure. Perhaps the process takes place under the influence of third bodies, called enzymes; maltase and diastase in the cases here cited being the possible agents (but see enzymes, p. 399). The starch accumulates in minute granules within the chloroplasts (fig. 649), so their stroma may be the direct agent in organizing the starch, or at least may be the seat for the formation of the enzymes which bring this about. These grains have a definite structure and a rather uncertain composition (see starch, p. 358), for both of which the chloroplast itself may be responsible (see leucoplasts, p. 389).

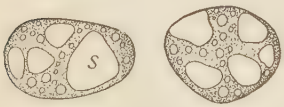


Fig. 649. — Two chloroplasts of *Rhipsalis*, with grains of starch (*s*) and minute oil droplets. — After Schimper.

Removal of products. — If a leaf is isolated, the accumulation of the synthetic products may reach a point where it interferes with further photosynthesis; but in nature this does not occur. Use on the spot, or diffusion of such products as remain simple and soluble, or the digestion of the more complex and the insoluble ones by enzymes (p. 399) and subsequent diffusion, is constantly removing the new materials from the leaves and stems to other places where they may accumulate or be used (see translocation, p. 393). In darkness or weak light, the transportation facilities, temporarily overtaxed in full light, overtake the manufacturing; the laboratories are cleared, consumers are supplied, and the warehouses and distributing centers are filled with the surplus awaiting future use.

The by-product.—The by-product, oxygen, is used to some extent in respiration (p. 406); the excess diffuses to the surface, whence it escapes into the aerating system and thence into the air. The final step in its exit can be observed in water plants readily, because the constant accumulation in the air chambers leads to its escape as bubbles when the passages are opened by a cut or break (fig. 650). If the canals are intact, O_2 may become abundant enough in bright light to form bubbles on the surface, which rise as they become larger. The rising gases can be conducted by an inverted funnel into a test tube and analyzed; they are about 85 per cent oxygen, the remainder being other gases produced in other processes. So uniform is the evolution of O_2 by water plants that with precautions the number of bubbles given off in unit time can be used to exhibit the general effect of the three external factors, intensity of light, temperature, and supply of CO_2, on photosynthesis. It is not satisfactory for quantitative determinations.

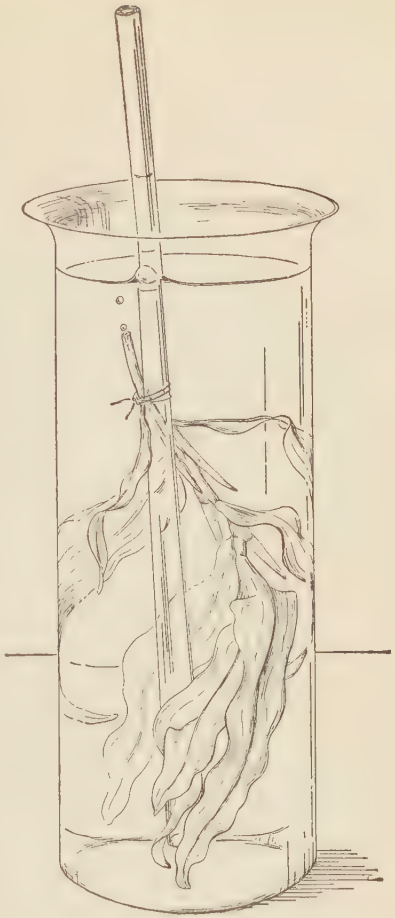


FIG. 650.—Upper part of a plant of *Potamogeton* attached to a glass rod and submersed, showing escape of gas bubbles (mostly oxygen) from cut end of stem in sunlight.

3. THE SYNTHESIS OF PROTEINS

Proteins the end-product.—The formation of carbohydrates is by no means the only process of food making. Indeed it may be looked upon as merely the first stage in the construction of proteins, of which carbohydrates are important components. As the living protoplasm appears

to be composed chiefly of proteins (probably more complex and labile than in the non-living state), it is evident that protein foods are of the highest importance — indeed indispensable — for nutrition, since it is the protoplasm which grows, wastes, and needs repair. Proteins are, as it were, the highest type of foods; they represent the final stage of food making.

Inasmuch as the carbohydrates contain only carbon, hydrogen, and oxygen, while proteins contain in addition nitrogen and sulfur and in many cases phosphorus also, it is plain that they cannot be formed from carbohydrates alone. A strict carbohydrate diet is as unsuitable for plants as it is for animals. Some materials must be supplied from which nitrogen, sulfur, and phosphorus can be obtained.

Source of nitrogen. — As the air contains 78 per cent of nitrogen, the atmosphere would appear to be a natural source of this element. But though the nitrogen is everywhere dissolved in the water of the plant, and can enter and leave it freely, no plants are known to be able to use it in this uncombined form, except certain bacteria, some of which live in the soil and in some waters. Certain soil species enter the roots of various plants, especially the Leguminosae, causing them to form tubercles. (See below, p. 379.) Almost all plants, therefore, must get combined nitrogen. This is found in soils as nitrates of various bases, *e.g.* calcium, magnesium, potassium, and sodium; and when a soil is deficient in nitrogen, such compounds are important constituents of the fertilizers, natural and artificial, which are added to it. The nitrates in the soil result mainly from the decay of organic matter in it. The later steps in the process are controlled by certain bacteria in the soil which bring about the oxidation of ammonia to nitrites, whereupon others oxidize the nitrites to nitrates. The very fertility of arable soils, therefore, depends on the microscopic organisms living in them, which prepare the way for the larger plants.

Loss of N. — The soil of cultivated areas is constantly losing its combined nitrogen by solution and drainage, and this loss is only partially made good by the ammonia and nitrous and nitric acids washed into it from the air by rains. Under natural conditions the dying vegetation ultimately returns its constituents to soil and air; but crops are carried off, their nitrogen with them. Gardens and fields, therefore, require replacement of this nitrogen sooner or later. When they lie fallow, certain bacteria of the soil, associated with algae and perhaps with other plants, slowly increase the nitrogen content of the soil by fixing

the free N_2 from the air in their bodies, which, dying, restore it to the soil.

Leguminosae. — The case of the Leguminosae and a few other plants is peculiar. Certain soil bacteria enter the young root hairs, grow and multiply, and work gradually into the cortex, where, as they increase, they stimulate the rootlet to multiply and enlarge the cortical cells, so that a local swelling or tubercle is formed. The largest of these scarcely exceeds the size of a hazelnut, and most are smaller than a pea or even a grain of wheat. The relations are probably as follows: The bacteria depend on their host for carbohydrate food, but can use the free nitrogen (presumably that nearest them in solution, which is replaced from the air) in their protein making. Being favorably situated, many of the bacteria become excessively enlarged, and often branch into X and Y forms.

The host sooner or later gets the better of the parasite and consumes these fat bacteria ("bacteroids"), their proteins proving valuable foods. By reason of this peculiar relation, leguminous crops can be grown in soils which contain no combined nitrogen whatever, provided the proper bacteria be present.[1] If the crop be then plowed under (a process called green manuring), the soil is enriched in nitrogen at the expense of the air.[2] (See further Part III on root tubercles.)

Source of S and P. — The sulfur and phosphorus needed are obtained by the green plants from sulfates and phosphates which dissolve in the soil water. Few soils lack these, though for cropping the phosphates may be insufficient or may be so reduced as to interfere with full development. "Land plaster" (gypsum, or calcium sulfate) is sometimes applied to fields; but it probably has more beneficial effects on other qualities than on the composition of the soil. Phosphates are an important part of artificial manures.[2] In the case of both nitrogen and phosphorus it is highly important, if immediate effects are desired, that the compounds be such as are "available," and compounds can be available only when they are soluble or readily become so.

Raw materials. — The nitrates, sulfates, and phosphates enter the larger plants through the roots. These are the mineral salts which are most necessary for the well-being of the plant, because they are needed for

[1] If not, the soil may be infected by scattering on it soil in which such a crop has been previously grown. Commercial attempts to supply pure cultures of appropriate bacteria for infecting the soil through the seed sown have not been very successful.

[2] The whole subject of the relation of manures and fertilizers to the soil and crop is in a very unsatisfactory state and needs further investigation before the practice and results can be explained.

protein synthesis. Like CO_2 and H_2O, they have been called "foods"; but it is far better to look upon them as raw materials out of which, with others, food can be made.

Given carbohydrates (finished and partly torn up again, or "in the making") plus nitrates, sulfates, and phosphates, most plants can make proteins. There is no set of plants to which protein synthesis is restricted, as is photosynthesis to the green plants. Yet there are plants (certain bacteria for example) which require their nitrogen supplied in other forms than nitrate, and some even which can use nothing less complex than proteins. Here we may properly speak of assimilation rather than of synthesis.

No special organs. — In the larger plants protein synthesis is not restricted to a particular organ. Neither chlorophyll nor light is essential to it, for it is carried on freely by fungi which have no chlorophyll, and it is doubtful, in spite of much experimenting, whether light has any influence upon its rate. Since carbohydrates are usually the basis of protein synthesis, the leaves, in green plants, are the chief seat of this process; for in the leaves carbohydrates are being made, and to them stream the dilute watery solutions of salts, brought *via* the xylem bundles by evaporation.

Process. — So long as the constitution of proteins remains unknown it will be impossible to describe the process by which they are made. Inasmuch as all proteins on decomposition yield amides (amino-acids), and the simpler ones are certainly formed from them by condensation, it is supposed that carbohydrates are converted into amides first, by the introduction of NH_2-groups here and there, and that these amides link themselves together, some becoming modified by the incorporation of sulfur and phosphorus molecules, and so form proteins of various kinds. But the details are all uncertain and only the vaguest statements can be made.

4. OTHER WAYS OF GETTING FOOD

Dependent plants. — The green plants are sometimes distinguished from others by the term *autotrophic*, meaning that they nourish themselves by their ability to make in their own bodies the most important foods, the carbohydrates. All others are *heterotrophic* plants, signifying that they secure food in a different way. (But see p. 362.) The more important ways are now to be described.

Among the many thousand species of heterotrophic plants, the bacteria and fungi hold the dominant place. A few seed plants lack chlorophyll entirely, such as the Indian pipe (*Monotropa*), beech drops (*Epifagus virginiana*), dodder (*Cuscuta*), etc.; and some have only partially lost it, or with a good supply nevertheless have the nutritive habits of the non-green plants.

The families in which such dependent species are prominent are the Loranthaceae, Rafflesiaceae, Scrophulariaceae, Orobanchaceae, and Balanophoraceae.

If a plant cannot make carbohydrates, it must of necessity get food directly or indirectly from some plant that can. The direct way of doing this is to live on or in a live green plant. The indirect way differs only in that the food secured is more remote from the original food maker. Thus, a plant may live upon or in some animal or some non-green plant, or upon the dead bodies of these, more or less decayed and disintegrated. Indeed, decay and disintegration are only the obvious evidence that plants (chiefly the minute bacteria and fungi) are living upon such a dead body. And not infrequently death itself is simply the result of the vigorous development of such creatures on or in the body of a once healthy organism.

Parasitism. — An association between two live organisms is known as *symbiosis*. When one obtains its food from the other, the relation is called parasitism, and the two are known respectively as *parasite* and *host*. As a rule the food maker is called the host, and the other the parasite; if neither or both be food makers, the larger is distinguished as the host. Thus, fungi are parasitic on leaves or twigs or in the wood of trees, or on animals; "beech-drops" (*Epifagus virginiana*, a small flowering plant) is parasitic on the roots of the beech tree; mistletoe is parasitic on elms, etc. This relation requires the closest contact between the cells of parasite and host, and the parasite even penetrates the cells of the host in many cases. The smaller parasites, such as fungi, may grow bodily through cells, doubtless dis-

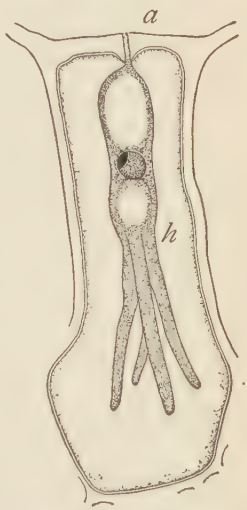


FIG. 651. — An epidermal cell of a grass (*Poa*) penetrated by a branched haustorium (*h*) of a fungus (*Erysiphe graminis*); the mycelial hypha to which the slender penetrating tube (*a*) is attached is not shown. — After SMITH.

solving the wall by some enzyme (see digestion, p. 399), or it may send into them short branches, called haustoria (fig. 651; see also figs. 1079, 1080, Part III), through which the food enters the parasite. A vascular parasite, the dodder, which twines extensively over coarse herbs, sends into its host short branches, likewise called haustoria (fig. 652), whose vascular strands come into the most intimate contact with those of the host. (See Part III on parasitism.)

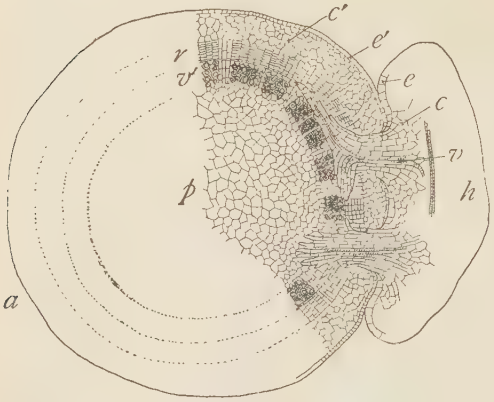


Fig. 652. — Section of stem penetrated by haustorium (*h*) of dodder (*Cuscuta*). — From Part III. (For explanation of letters, see fig. 1082.)

Partial parasites. — When such complete contact has been established, it is difficult to determine what or how much material migrates from host to parasite. Colorless parasites, of course, must get all their food from the host. Certain green parasites undoubtedly could live by getting merely water and its dissolved salts, for they can make food for themselves. Hence they are known as partial parasites. But that they completely restrict themselves to such food materials and do not admit any real food is quite improbable, in view of the intimate union between the two.

Fig. 653. — Ectotrophic mycorhiza of European beech (*Fagus sylvatica*); *h*, hyphae. — After Frank.

Mutualism. — The support of the parasite by the host may result in no considerable injury or even weakening. Indeed, many cases have been described in which the association suggested a partnership, whence the term *mutualism*. From another point of view the relation resembles that of master and slave, whence the term *helotism* (see Part III). The lichens (p. 78) furnish the classical example. Yet even here the algae are somewhat restricted in development by the constant drain upon them, though perhaps they can work at food

making longer because the encompassing fungus by its spongy texture retains rainwater longer than would the algae alone. Mycorhiza is another instance of so-called mutualism, in which fungi associate themselves with the roots of certain plants, especially the oaks (Cupuliferae), the heaths (Ericaceae), and the orchids (Orchidaceae). Sometimes they jacket the rootlets with a weft of filaments (ectotrophic mycorhiza, fig. 653), and sometimes they penetrate the cortical cells, forming a tangle about the nucleus (endotrophic mycorhiza, fig. 654). The fungi are supposed to aid the root in acquiring water and food materials (especially nitrogen compounds, which they themselves may form from the free nitrogen of the air) from the soil. Certainly they derive some food from the root, and injury to the root is suggested by its stubby form and the frequent absence of root hairs. In fact, the more the cases of so-called mutualism are studied, the more it becomes evident that they are only cases of modified parasitism, with minor injury to the host. (See Part III on reciprocal parasitism.)

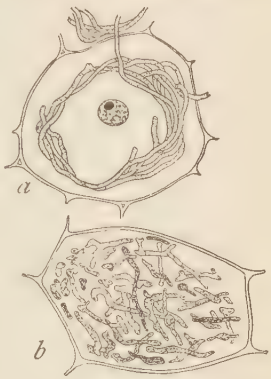


FIG. 654. — Endotrophic mycorhiza of *Neottia*: *a*, host cell with active fungus hyphae; *b*, cell with degenerating hyphae. — After MAGNUS. (See also figs. 1106, 1107.)

Injury by parasites. — On the other hand, the drain on the food resources of the host may be severe, so weakening it that it succumbs to adverse conditions which otherwise could be overcome. Quite apart from this weakening for lack of food, the parasite may act as a stimulus to local growth, or it may produce injurious substances which cause local or even general death. The location of a parasite is often marked by deformities; leaves are crinkled or thickened, as in peach curl; circumscribed swellings of peculiar and fantastic or beautiful forms (galls) grow on leaves or stems (fig. 655); even large tumors are formed, as in the black knot of cherry and plum trees. Local death is another common mark of the presence of a parasite. The fire blight of apple and pear trees, due to parasitic bacteria, gets its name because young shoots are killed for a distance of 20 to 50 cm., and the withered brown leaves make the tree look as though it had been scorched by a fire. General death in large plants is seldom produced by a parasite unless it interferes with the water supply or invades the entire organism. In wilt disease the parasite blocks the tracheae, interfering with the supply of

water to the leaves, and death follows with surprising suddenness. In other cases, since in plants there are no means for quick distribution of poisons locally produced, nor any regulatory centers whose injury upsets the whole system, death is likely to be merely local. In animals, on the contrary, a parasitic plant, restricted to a limited region, may produce poisons which are quickly spread through the body by the blood, attack the central nervous system or important viscera, and soon cause death. Thus, in diphtheria, the bacteria flourish chiefly

FIG. 655. — Galls: *a*, on leaf of rose; *b*, on stem of grape. — From PART III.

in the throat, where they may produce no serious lesion, but the toxins produced reach the heart and kidneys and sometimes fatally injure them.

Saprophytes. — The association of a plant with a dead organism or organic débris is called saprophytism, and the live member is a saprophyte. Since a parasite may kill its host and then continue to live upon the body, the distinction between parasites and saprophytes is not always clear. Thus there are obligate parasites and obligate saprophytes; plants, namely, that are obliged to live in one relation or the other. Correspondingly there are facultative parasites and facultative saprophytes, which may pass part of their lives in one way and part in the other or wholly in either. Often the full cycle can be completed only if the given plant can establish the preferred relation.

Saprophytes are very numerous and varied. They may be superficial, or may penetrate the substratum thoroughly, showing finally at the surface only the reproductive bodies. The very fact that they are getting food from the dead organism indicates that they are consuming it. Inasmuch as they often must digest the food before it can enter their bodies, they disintegrate the body on which they feed. In the course of this digestion and disintegration, many and varied chemical reactions occur, some incited by the saprophyte, some incidental to the changes it produces. These are summed up for fluid media under the term *fermentation*, and for solids under the terms *decay* or *putrefaction*. Certainly in fermentation (p. 409), and probably also in putrefaction and decay, some of the most striking reactions are not connected with food getting, though apparently they are entirely similar thereto.

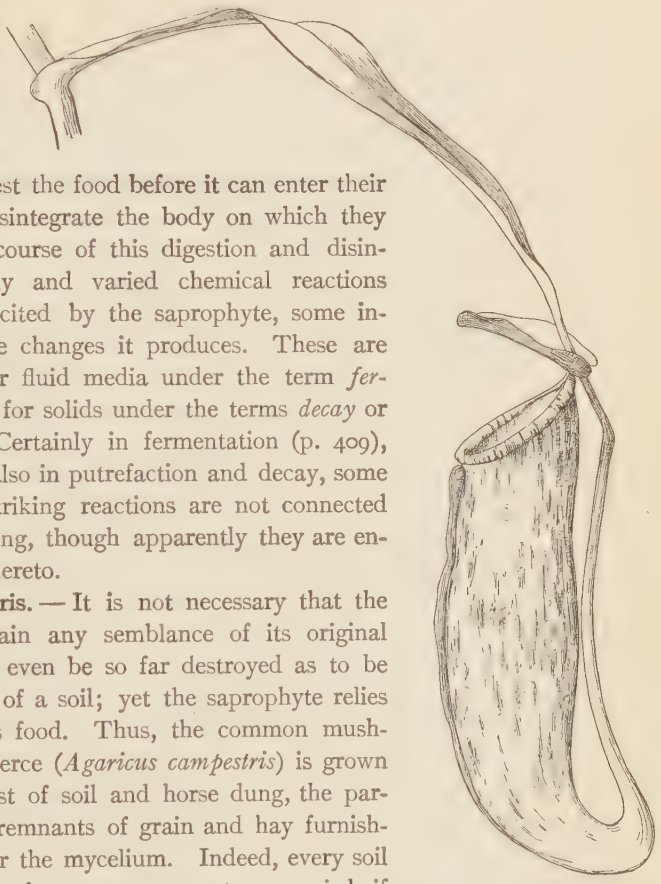


FIG. 656. — Leaf of *Nepenthes Mastersiana*. — From a photograph by G. W. OLIVER.

Organic débris. — It is not necessary that the dead body retain any semblance of its original form. It may even be so far destroyed as to be mere particles of a soil; yet the saprophyte relies on these for its food. Thus, the common mushroom of commerce (*Agaricus campestris*) is grown upon a compost of soil and horse dung, the partially digested remnants of grain and hay furnishing the food for the mycelium. Indeed, every soil containing organic matter supports a varied if minute flora, whose operations are often indispensable to the welfare of larger plants.

Succession. — Nothing is more striking than the succession of saprophytes that live upon a dead organism and finally dispose of all its organic matter, each appropriating a suitable part and reducing that to the most simple and stable compounds, until finally it "returns to the dust whence it came." This emphasizes, too, the striking differences

between saprophytes in their use of offered foods — differences which at present are quite inexplicable. A classification of saprophytes according to the sort of food on which they thrive best has been made; but this expresses only in a summary way our very imperfect knowledge of their nutrition.

Insectivorous plants. — Besides the ordinary parasites and saprophytes, there are a few rather isolated cases of green seed plants which

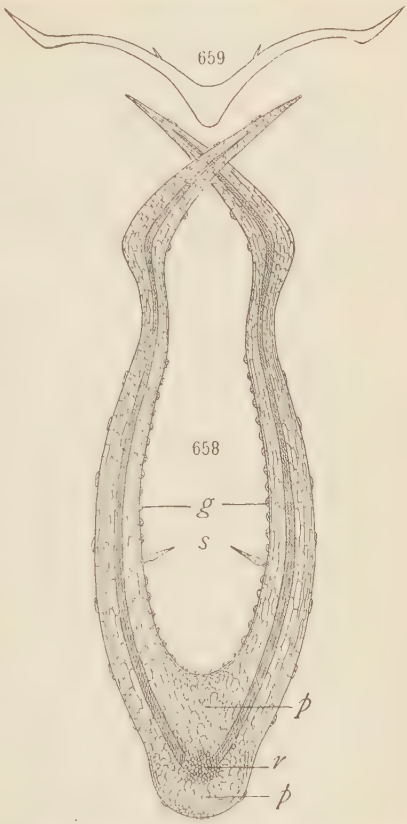
FIG. 657. — A rosette of leaves of Venus's flytrap (*Dionaea muscipula*) seen from above. — From a photograph by G. W. OLIVER.

have special apparatus for capturing small animals and digesting them. Some are submersed water plants, some grow on land. They are collectively known as insectivorous or carnivorous plants, but the methods of capture are quite diverse.

Pitcher plants. — The pitcher plants, *Sarracenia*, *Darlingtonia*, *Nepenthes* (fig. 656), and *Cephalotus*, have part or all of the leaf trumpet-like, pitcher-like, or cuplike, holding more or less water. The sides have stiff downward-pointing hairs, slippery areas of treacherous footing, decep-

tive translucent spots away from the concealed opening, one or all, which prevent the escape of insects that wander in and sooner or later drown in the fluid; whence nitrogenous compounds derived from their bodies by decay or digestion enter the tissues of the pitcher.

Flytrap. — Venus's flytrap (*Dionaea*, fig. 657) has leaves with two terminal lobes about 1 cm. long, hinged about the midrib, and fringed with long slender teeth, which interlock when the lobes shut together (figs. 658, 659). On the surface of each lobe are three large sensitive bristles, and if one of these be bent so as to compress the basal cell, the lobes shut like the two jaws of a trap. Insects, flying or crawling, which come into contact with the bristles are often caught. Then the glands upon the upper (inner) surface pour out a digestive fluid, the proteins are reduced to such simplicity that they can enter the tissues, and after a few days the leaf opens again. Its water mate, *Aldrovanda*, has a similar but smaller trap, by which minute swimming crustaceans, *Daphnia*, *Cyclops*, etc., are often caught.



FIGS. 658, 659. — Cross sections of the terminal lobes forming the "trap" of *Dionaea*: 658, enlarged view, closed position, diagrammatic; *g*, digestive glands; *p*, *p*, parenchymatous tissues whose varying turgor opens and closes the "trap"; *s*, sensitive bristles; 659, outline, on a smaller scale, of same in an open position. — After KNY.

Sundew. — *Drosera*, the sundew, has its leaves (fig. 685) fringed and covered above with stalked glands that secrete a viscid transparent fluid, in which small insects alighting may become enveloped by their own struggles, and further (in our species) on account of the inflection of the stalks of the glands. When an insect is caught, the character of the secretion changes; it becomes more watery and

contains an enzyme which digests proteins. That the products enter the plant and are advantageous has been shown by comparing fed and unfed plants in the same pot. Those on whose leaves tiny bits of meat and egg were placed were larger and thriftier, and had more flowers, as well as more and larger seed, than the ones which grew under identical conditions without feeding.

The capture of insects probably supplements a scanty supply of nitrogen obtained from the soil nitrates; but too little is known of the ecology of such plants to establish this explanation as at all conclusive

A fuller discussion of most of the topics of this chapter will be found in Part III.

5. THE STORAGE AND TRANSLOCATION OF FOOD

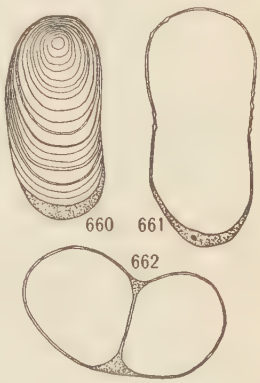
Surplus food. — A part of the food made by a plant is promptly utilized in the making of new tissues (growth) and in the repair of the protoplasm which has undergone changes in the course of its activity. It is often said, also, that a part of it is oxidized directly to furnish energy for growth and other work; but it is at least doubtful whether this is true.[1] However that may be, most plants, at least at some period of their existence, make more food than they actually use at the time. The surplus is then stored for a longer or shorter time, until it is required. But it may never be used.

Storage places. — Accumulation may take place in the very part where the food is made; but usually, if there is any room there, it is insufficient; and to judge from the infrequent storage in food-forming organs these two functions are not fully compatible. So when there is any considerable surplus of food, it migrates to some more or less specialized storage organ. In the lower plants these are relatively simple, for ordinarily such plants make little excess food. In *Marchantia*, for instance, the colorless parenchyma of the lower part of the thallus is accounted the storage region. In the pteridophytes and spermatophytes, any one of the larger organs, root, stem, or leaf, may become the seat of food accumulation. In many cases there is marked change in structure and form.

Parenchyma increased. — The characteristic change in structure consists of an exaggerated development of parenchyma, in which chiefly the

[1] The matter will be discussed further in the section on Respiration, p. 403.

food accumulates. This may be the parenchyma of the cortex, or of the vascular bundles, or of the pith; or all may be involved. One noteworthy point is that the storage tissues are composed of live cells, even though, as in some ferns, they are very thick-walled. It is to be observed also that the reservoirs of food are usually located in parts that persist through a dry or cold season unfavorable to growth, and that have rudimentary growing points capable of quick and vigorous development by using the adjacent surplus. So the seeds, bulbs, tubers, rhizomes, etc., are organs of propagation, and by way of attaining that end become also organs of storage. (See Part III on seeds, bulbs, and tubers.)



FIGS. 660–662. — Starch grain and leucoplasts of *Pellionia:* 660, simple starch grain with leucoplast in position; 661, leucoplast alone of a similar grain; 662, leucoplast of a twin grain. × 900. — After MEYER.

Storage cells active. — The storage of food is not merely a stuffing of passive cells with surplus food; it involves the activity of the storage cells themselves, at least for the accumulation of the food, and usually also for the mobilization when this food is about to travel to growing regions where it is subsequently used. The process of mobilization is commonly called digestion (see p. 397), and seems to be the reverse of the process by which the storage forms of food are produced.

Storage forms. — The storage forms of food are chiefly starches, sugars, hemi-celluloses, inulin, fats, and proteins. From this list it will be apparent that carbohydrates predominate, and quantitatively they form much the greater part of stored food.

Starches. — Starches are stored in the form of grains, many having a form characteristic of the plant in which they are found. The grains are organized by the activity of cell organs called leucoplasts or amyloplasts (figs. 660–662), which seem to take the material as it comes to the cells, perhaps as glucose, and combine it into larger and more complex molecules, that finally become starch. This is disposed in the interior of the leucoplast as one or more grains, which at length stretch it enormously, or even rupture it. The actual structure of the grain is believed to be that of a spherite; that is, it is composed of a multitude of microscopically minute, threadlike crystals, radiating from its organic center. If

more than one such crystal starts in the leucoplast, a compound or aggregate grain may result (fig. 662). The grains may show irregular layers (fig. 660), this appearance signifying differences in the proportion of water, composition of material, etc., doubtless determined by variations in the available sugars and other conditions during the growth of the grain.

The starchy reservoirs are sources of important foods for men and animals, as well as plants. Many of our farm and garden crops are such storage organs, greatly improved and enlarged by breeding. Potatoes, sweet potatoes, yams, all the cereals, peas and beans, arrowroot, sago, and tapioca are widely used plant products, whose most abundant constituent is starch. The extraction of starch for commercial purposes, especially from potatoes and corn, is an industry of considerable magnitude, as is also the production of alcohol by the fermentation of glucose derived from the starch of these plants. The following table shows the approximate starch content of some common food reservoirs, in percentages of their dry weight.

In seeds of rice	68	In seeds of navy beans .	45
In seeds of wheat	68	In seeds of flax	23
In seeds of corn	60	In seeds of almond . . .	8
In seeds of pea	52	In tuber of potato . . .	80

Sugars. — The chief storage form of the sugars is saccharose, or cane sugar. While glucose and fructose may be counted as constituents of almost every active cell, they do not accumulate in nature to any great extent, whereas saccharose in some plants, such as sugar cane and beet, is almost the only form of surplus food, and in many it accompanies the reserves of starch. The commercial supply of sugar is obtained chiefly from cane and beet, while sorghum, maple, and certain palms furnish a relatively small or local supply.

Sugar is extracted from cane by crushing and washing, clarifying the liquor and concentrating it. Beets are finely sliced and the sugar is extracted by diffusion, then recovered by clarification and concentration of the solution. The cultivated races of beet now average nearly 15 per cent of sugar, with some samples going over 20 per cent, as against less than 7 per cent when breeding began. Cane juice yields 10–18 per cent, and maple sap 2–5 per cent of saccharose. The refining of sugar by redissolving and purifying removes the coloring and flavoring matters which give to crude sugars from different plants their distinctive taste.

"**Reserve cellulose.**" — This name has been applied to food accumulated upon the walls of cells; yet the substances are quite different from the cellulose which forms the permanent part of the wall, and should rather be called *hemi-celluloses*. They consist often of mannans and galactans, which on digestion yield mannose and galactose, sugars that are quickly

transformed into other compounds. The hemi-celluloses are especially common in the endosperm of seeds, and are used as food by the embryo in germination. They are deposited in layers on the interior of the cell walls, sometimes to the great reduction of the lumen; yet through the pits in the thickened walls the protoplast in each chamber maintains communication by slender threads with its neighbor. This excessive thickening imparts to such seeds a hornlike toughness, as in the coffee "bean," or even a bony hardness, as in the date "stones." Sometimes cotyledons and even bud scales have like deposits on their cell walls.

Inulin. — Inulin is comparatively restricted, being characteristic of a few large families (and occasional elsewhere). It occurs dissolved in the cell sap, especially of subterranean organs. It is a very complex carbohydrate, though less so than starch, having a formula $n(C_6H_{10}O_5)$, where n is probably as much as 12 or 18. Whereas starch is built from glucose units, inulin is formed by the condensation of fructose units, and is comparable in complexity with some of the dextrins, which starch yields by digestion. When inulin-containing tissues are put into strong alcohol, the inulin is deposited as spherites (see Part III, fig. 1209).

Fats. — Fats are among the most important and valuable of surplus foods. In most plants they exist as small drops of oil in the protoplast; but in some cases, as in cacao, they are solid at ordinary temperatures. The most universal storage place for fats is the seed, where it is in some cases the dominant form of food, and in almost all it is present in greater or less quantity. It is by no means confined to seeds, but occurs in the flesh of fruits (olive), in rhizomes (potato, iris, and sedges), in bulbs (onion), and in roots (carrot). In almost every part of a plant, indeed, small quantities of oil may be found, and from many reservoirs it can be extracted in commercial quantities.

True oils must be distinguished from volatile or essential oils, which are common in leaves and flower parts. The latter usually have a distinct odor and make a temporary translucent spot on writing paper, whereas that made by true oils is lasting.

Accumulated oils are obtained for commercial uses by crushing and pressure; but as only a portion of the oil (which forms 2 to 68 per cent of the dry weight) can be recovered thus, the "cake" remaining, with its residue of oil and other substances, may still be valuable food for animals, as is the case with cotton and flax seed.

Proteins. — Proteins, unless they take on a specific solid form, cannot readily be distinguished from resting protoplasm. Thus, the "gluten"

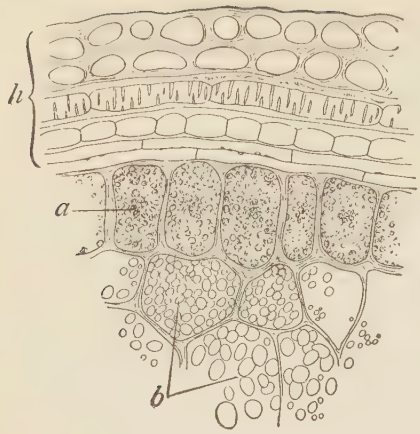


FIG. 663. — Outer portion of a cross section of a wheat grain: *h*, various integuments of the ovary and seed, forming the husk; *a*, cells of "aleurone layer" of endosperm, loaded with protein grains; *b*, starch-bearing cells. — After COBB.

of wheat is apparently a part of the network of protoplasm in which the starch grains are imbedded. The best known storage forms appear in vacuoles of the endosperm in seeds. The proteins accumulate in the small vacuoles, and upon the loss of water, characteristic of maturation for a resting period, become more and more concentrated, until finally they solidify, forming the "aleurone" or protein grains. These are very commonly associated with reserve starch, either in the same cells, as in the pea and bean, or the protein grains are characteristic of certain cells, as in wheat and other cereals, where they abound in the outer layer of the endosperm (fig. 663). In large grains some proteins may crystallize out, as in the castor bean (fig. 664) and the Brazil nut, but oftener they remain apparently homogeneous.

Amides. — Amides occur in such quantities, especially in some sappy reservoirs, that they may be considered as stored food. There they may form 40–70 per cent of the nitrogenous materials.

Alkaloids. — Some recent studies of cacao ("cocoa") and coffee make it probable that their alkaloids (see p. 415), which are of a different type from most, may be a form of surplus nitrogenous food, since they come again into use. They constitute a very compact source of available nitrogen.

Combination of food. — It must not be supposed that the foods above named accumulate independently. On the contrary, they always occur associated, though one form is likely to be dominant. Rarely, if ever, are they so re-

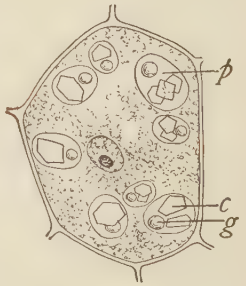


FIG. 664. — Cell from endosperm of castor bean (*Ricinus communis*): *p*, *p*, protein grains, made up of amorphous proteins, crystalline proteins (*c*) ("crystalloids"), and globular compounds of proteins with calcium and magnesium, the globoids (*g*). — Adapted.

lated to one another in amount as to form what animal feeders call a balanced ration. This is shown by the fact that, when growth is resumed, food of one sort is not used in the ratio which it bears to others stored with it. Often indeed the reserves are not exhausted until the plant or shoot, having begun independent manufacture, is able to supplement the deficiencies in the stored ration. Thus, finally, it may utilize all the accumulated reserve, but often this is not done, and the excess is again stored elsewhere.

Traveling forms. — Since the places of storage are seldom the places of food making or use, translocation of food usually precedes and follows storage. Unfortunately, little is known about the translocation of foods. It seems clear that the traveling forms must be relatively simpler than those in which they are stored. Obviously, they can travel only in solution, and, as a rule, the protoplasm does not permit the passage of the foods in their storage forms. Thus, cane sugar probably travels as glucose and fructose; the fats as glycerin and fatty acids; the proteins as amides. For in all translocation of foods, whether in small plants or large, it is necessary that they be able finally to diffuse through live cells, and the more complex compounds are usually unable to do this.

Diffusion. — In the smaller plants osmotic differences alone must account for the transfer from cell to cell. This may be facilitated by the delicate protoplasmic connections which commonly exist and would make it unnecessary for all the food to pass through the cell wall itself. In fungi which have coenocytic hyphae, the absence of transverse partitions probably facilitates transfer; while the surging movements that have been observed in the contents of certain molds (Mucorales) would certainly do so. Yet actual knowledge regarding the translocation of food in even the simplest plant is scanty. Food obviously gets from place to place, and there is apparently no way for it to do so except by diffusion.

Conducting system. — In the larger plants a conducting system is developed; and it is evidently advantageous that the slower movement of diffusion be supplemented by a more rapid one along the chief lines of travel when the factories are separated by considerable distances from the places of use or storage. This conducting system in all the vascular plants consists of the phloem strands. It may be supplemented in certain large families by the latex system, though the function of the latex is somewhat uncertain.

Phloem strands. — The phloem strands are usually definitely related to the xylem strands (which carry water), though they occur also independent of them. In most seed plants there is a phloem strand lying along the outer face of a xylem strand, and except in the monocotyledons there is generally between them a meristem (cambium), which may add to the radial diameter of both xylem and phloem. It may also, if it extend from one strand to another around the axis, produce new secondary phloem strands between the old ones. The phloem strands form a continuous system, and may be traced from the stem outward into the leaves and downward into the roots. So followed, they usually disappear before the xylem strands end; that is, their differentiation does not begin so early in the rootlets nor extend so far in the leaves.

Elements of phloem. — The elements of the phloem strands are sieve tubes, companion cells, cambiform cells, and parenchyma, with sometimes mechanical tissues, though the latter belong more commonly to the adjacent tissue systems. It is impossible to specify the precise rôle of each of the elements; but among them all the sieve tubes may be considered the chief lines of conduction, the others being supplementary thereto.[1] In a way the sieve tubes are analogous to the tracheae of the xylem; particularly in that, having their end walls partially resorbed, they constitute tubes through which the foods may move without the delay necessitated by osmotic transfer from cell to cell.

Evidence of conductivity. — The reasons for assigning conductive functions to the phloem strands are chiefly these: (1) The pith is so commonly dead and its cells filled with gases that it may be excluded from consideration. (2) The cortex, too, is often dead; particularly is this almost universally true of the older parts of shrubs and trees in which it is frequently sloughed off after a few years; yet there is an active transfer of foods. Moreover, the movement of food through the protoplasmic membranes of live cells is apparently too slow to meet the needs of plant growth. (3) When the cortex is removed by surgical operation, the supply of food seems to be quite adequate to permit development; but if the phloem strands are interrupted, transfer of foods is almost or quite stopped.

This is particularly noticeable when girdling occurs in nature, as when birds destroy a zone of bark in conifers whose wood remains able to conduct water. The tops and roots (if one or more circles of branches below the injury remain,

[1] It is as though the sieve tubes were the main railway lines and the adjacent tissue sidetracks temporarily occupied.

keeping the latter supplied with food) may continue to live for years (fig. 665), yet the vigorous growth is above the injury. Girdling experiments with willow shoots are often cited as adequate proofs of the conductive function of phloem. For example, by removing a ring of cortex 5 mm. wide, a few centimeters from the lower end in one case and several times as far in another, and placing both shoots in water, lateral roots and shoots develop in both cases. Their vigor is somewhat proportional to the relative lengths of stem below and above the girdling, and this is taken to indicate that the new parts can draw only upon food stored in the part of the stem above and below the girdling, transfer being prevented by the interruption of the phloem. But if bridges of bark be left across the gap, the differences of development tend to disappear; and the more numerous the bridges the less the differences. While such experiments agree fairly well with other observations, they are in themselves not conclusive, since the results are complicated with obscure phenomena of regeneration, and perhaps with wound irritability.

FIG. 665. — Portion of the trunk of a pine, the bark completely destroyed by birds at *a*. A single circle of branches below keeping all the parts lower than *a* scantily supplied with food, the upper part made an excessive growth, especially in the neighborhood of the wound, but food could not pass *a* freely (perhaps not at all). Original in the museum of Purdue University.—From photograph supplied by STANLEY COULTER.

(4) The content of the sieve tubes, which is a coagulable slime, consists more largely of foods than would be at all likely unless the sieve tubes were organs of either conduction or storage, and the latter supposition is unlikely because the foods are almost entirely in solution. In a typical case analysis showed that, excluding water, the constituents were: carbohydrates, 30 per cent; amides, 38 per cent; proteins, 20 per cent. So rich a supply of soluble foods could hardly be found anywhere else. (5) A bit of merely corroborative evidence is derived from the distribution and relative development of the phloem. No plants need more facile movement of foods than vines, whose stems are necessarily slender and long, and in none is there better development of the phloem. Indeed, when the anatomist wishes to study the largest and most specialized sieve tubes, vines are almost invariably selected. Moreover, where the requirements for food transfer are the greatest, as in flower clusters and in the branches of inflorescences, the phloem strands are particularly well developed.

Rhythmic translocation. — Since leaves are the principal regions of food making, which is distinctly rhythmic by reason of the alternation of light and darkness, the translocation of food shows a corresponding rhythm. The transfer of any soluble food is continuous, and the rate is determined by the usual factors; but, as the transportation facilities are overtaxed during the day, there is on the whole an accumulation of food in the leaves then; only after the nightly slackening does emptying of the leaf become obvious.

That a leaf which shows starch near the close of a day may show none in the early morning does not necessarily indicate that carbohydrates have been carried off during the night, though they doubtless are, but only that they have been reduced in amount in some way, probably by migration and by conversion into other foods.

Causes of movement. — Nothing is satisfactorily known as to the causes of movement in the phloem. In the sieve tubes the absence of protoplasmic membranes closing the ends surely permits more rapid diffusion, which may be further facilitated by mechanical mixing due to bending and other compression of parts of the system. That the contents are under pressure is shown by the rapid oozing of material from cut sieve tubes, an amount being reported in *Cucurbita* which indicates that one or even two internodes had been emptied, and so the material must have passed 75 to 100 of the sieve plates (the perforate end walls of the sieve cells). The source of this pressure and the effect of it on translocation is not known.

Latex system. — In certain families,[1] it may be that translocation of foods takes place through the latex vessels, as well as by the phloem. Latex vessels form a system of branched or anastomosing tubes running through the cortex (more rarely elsewhere), and ending blindly in the leaves and roots. Histologically, they are coenocytes or cell fusions (see Part I, p. 27). They approach very near to the growing points, and in the leaves have close relations with the manufacturing cells, the very arrangement sometimes suggesting its fitness for collecting foods. The latex which fills these tubes is the cell sap of a huge vacuole, the protoplasmic contents being reduced to a very thin layer. Latex is in part a watery solution of many substances, such as proteins, sugars, gums, tannins, alkaloids, and salts; in part an emulsion of oils and tannins in droplets; and in part suspended granules of starch, gum,

[1] Particularly the Papaveraceae, Compositae (Cichorieae), Lobeliaceae, Campanulaceae, Asclepiadaceae, Apocynaceae, Euphorbiaceae, Moraceae, Araceae, and Musaceae.

resin, and caoutchouc. Some latex is translucent, but usually it is an opaque, white, yellow, or orange liquid, familiar to many as the milky "juice" of dandelion, poppy, milkweed, or the orange "blood" of the bloodroot. Latex is commercially important as the source of opium and its alkaloids, of India rubber, and of gutta percha.

Function. — The principal reasons for ascribing to latex vessels the function of a conducting system are the abundance of foods in the latex, and the peculiar structural relations of the latex vessels to the nutritive cells of the leaves. The carbohydrate and nitrogenous foods of the latex run as high as 30 per cent of the dry matter therein; they are most abundant when active growth and development are beginning, and least so when growth is checked and a resting period is at hand. In some leaves the latex vessels look as though they were favorably arranged to receive materials collected from the nutritive cells. Yet for the conductive function the evidence is rather presumptive than convincing. It may be that the latex has to do rather with storage and protection.

For further details on latex and accumulation of foods, see Part III.

6. DIGESTION

Nature of digestion. — Whenever foods are insoluble in water (as are some of the most valuable ones), they cannot be used by plants until transformed into a soluble substance. Whenever soluble foods are unable to diffuse readily through protoplasmic membranes, they can scarcely move from one point to another, and are available, if at all, chiefly in the cell where they happen to be. Every transformation of food by the agency of a third body from an insoluble to a soluble and from an indiffusible to a diffusible condition, whatever the precise chemical nature of the change, is summed up in the term *digestion.* This use of the term is in exact accord with its long use in animal physiology. The processes in plant and animal, indeed, are essentially the same; they are wrought by the same sorts of agents, affect the same sorts of substances, and result in the same sorts of products.

No special digestive organs. — Plants differ from the larger animals in having no pouched tube wherein food is lodged, and in which some of the more striking digestive processes take place, before the food truly enters the body. This digestive tract, its parts and accompanying glands, constitute the special digestive organs of the animal, though much important digestion takes place elsewhere. Plants have no special

digestive organs comparable to these; but places of food making and food storage must be places where digestion is also particularly active.

Misleading comparisons of the leaves to the stomach not rarely occur in primary books, which thus seek to "explain" the work of a leaf. When, as in one notable instance, a leaf is compared to a *kitchen*, where the dilute "soups," coming up from the roots, are "boiled down"; later to a *stomach*, where the food is made ready; and finally to the *lungs*, by which the dear little plant breathes, the child would have a truly appalling notion of a leaf were he not usually immune to such bad pedagogy, by reason of his ignorance of at least the stomach and lungs.

Extra-cellular digestion. — In plant as in animal, many foods must be digested before they can enter the cells at all, while others are digested as they lie in the cells. So one may distinguish, as to location, extra-cellular and intra-cellular digestion; but agents, processes, and results are essentially alike in both. In a fungus which merely pushes its way among the intercellular spaces of another plant, it is impossible to say whether any food is being digested or whether only what is already soluble and diffusible is being used. But when a fungus sends a branch, as a *haustorium*, through the cell wall (fig. 651), or when, as in certain wood-destroying fungi, the mycelium penetrates the walls freely in all directions, it is obvious that by some means the wall is actively dissolved at the point of contact.

Chemical changes. — The changes characteristic of digestion result in the cleaving of compounds into two or more simpler substances, with or without the taking up of water. In case water is incorporated the cleavage is called hydrolysis.

Thus when cane sugar is digested:

$$\underset{\text{saccharose}}{C_{12}H_{22}O_{11}} + \underset{\text{water}}{H_2O} \rightleftarrows \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\text{fructose}}{C_6H_{12}O_6}$$

Starch when digested takes up water, and four fifths of it breaks up into maltose units ($C_{12}H_{22}O_{11}$), the other fifth resisting full digestion for a long time. The maltose is further digested into two units of glucose, with assumption of another molecule of water. Other foods split up into simpler compounds without adding anything to their members. Thus sinigrin, a glucoside characteristic of the plants in the mustard family, cleaves thus:

$$\underset{\text{sinigrin}}{C_{10}H_{18}NKS_2O_{10}} \rightleftarrows \underset{\substack{\text{allyl thiocyanate}\\ \text{(mustard oil)}}}{C_3H_5CNS} + \underset{\text{glucose}}{C_6H_{12}O_6} + \underset{\substack{\text{potassium-hydrogen}\\ \text{sulfate}}}{KHSO_4}$$

The chemical changes of digestion represent only a few of the multitudinous reactions going on in the plant. The rate of these reactions, like all others, depends on temperature, concentration, etc., and espe-

cially on the effect of other substances which are present. It is not always evident just how a third body affects the rate at which one substance is converted into another in a chemical reaction, and so doubtless many effects of this sort pass unnoticed. But when the effect is pronounced, the third body is spoken of as a *catalyst*, and the effect of the catalyst on the reaction is known as *catalysis*. By such agents reactions, so slow as to be unnoticed, may be greatly accelerated and become evident; and others, which might be very rapid, are retarded, even until they are negligible.

Enzymes. — Among the catalytic agents (which are varied and not at all confined to living beings) are certain substances produced by organisms and called *enzymes*. These are widely different in their action, though they all seem to be of protein nature, so far as their chemical character is made out. The great difficulty in doing this lies in the impossibility, up to date, of separating them from the other proteins of the cell and obtaining them in any certain state of purity. In general they act best within certain narrow limits of temperature, such as 30–45° C., and most are totally destroyed at such temperatures as 60–75° C. Small quantities of free acid or alkali may facilitate their action; while certain metallic ions, *e.g.* Hg, Cu, Ag, may retard or inhibit their ordinary effect, just as they "poison" a live cell.

There seems to be a great variety of enzymes, each producing an appropriate effect upon certain foods; but others are known which have to do with reactions quite apart from the digestive changes. The *digestive* enzymes, then, are only part of a larger class of bodies, whose number and variety are only imperfectly known.

Reversible action. — The action of a number of enzymes is known to be reversible; *i.e.* they not only, under certain conditions, hasten the otherwise imperceptible decomposition of a particular substance into two or more simpler compounds, but also, under other conditions, accelerate the combination of the simpler substances into the more complex one. Indeed, it seems likely that the constructive action of enzymes may soon be shown to be as important as the destructive. This action would be of the greatest importance in the making of complex foods from simpler ones, such as the formation of starch from glucose, of cane sugar from glucose and fructose, of proteins from amido-compounds, etc. But the knowledge of this constructive action is yet very scanty.

Carbohydrate enzymes. — *Diastase* is one of the most important and widespread enzymes. It is found in practically all parts of plants, but

especially in leaves and storage organs. It partly digests starch into maltose, a residue, representing about 20 per cent of the grain, resisting its action for a long time. In the course of decomposition, various dextrins are produced by successive cleavage, presently becoming simple enough to be analyzed. The last member of the series breaks into maltose and isomaltose, $C_{12}H_{22}O_{11}$. There are at least two forms (possibly more), secretion diastase and translocation diastase, differing in the mode of dissolution of the starch grain. The former erodes the surface irregularly, whence narrow canals penetrate the interior, and the grain often falls into fragments; the latter corrodes the grain almost evenly, reducing it gradually in size until it disappears.

It is probable that what is here called diastase consists of at least two enzymes; *amylase*, which digests starch to a dextrin, and *dextrinase*, which breaks the dextrin into maltose; this, *maltase* (see below) cleaves into glucose.

Invertase, in like manner, can hasten the hydrolysis of cane sugar into two hexose sugars, glucose and fructose.

Trehalase and several other enzymes in fungi attack trehalose and other sugars peculiar to them, and digest them into the hexoses of which they were originally built.

Maltase, an enzyme which is often associated with diastase, carries the process of starch digestion further, cleaving each maltose molecule into two molecules of glucose.

Inulase likewise attacks inulin, breaking it up into levulins and finally into fructose. Perhaps there is here also more than one enzyme at work.

Cytase is responsible for digesting hemi-celluloses (chiefly mannans and galactans) of seeds, while enzymes under the same name, but probably different, have been found in wood-destroying fungi, and have been assumed present whenever a tissue is penetrated by a hypha, or by a more massive member, as in the sinking of the foot of bryophytes into the gametophyte (see Part I, p. 108) and in the emergence of the branches of roots through the cortex (fig. 667; see also Part I, p. 250, and fig. 558).

Fat enzymes. — *Lipase*, perhaps of several different forms and so deserving distinctive names, has been found in organs where fats are present, especially in seeds and many fungi. Lipase breaks up fats into their components, fatty acids and glycerin, which are then readily diffusible.

Glucoside enzymes. — These are common, setting free glucose from many different compounds. *Emulsin*, for example, breaks amygdalin, a glucoside common

in peach, almond, and apple seeds, into hydrocyanic acid, glucose, and benzoic aldehyde, thus:

$$\underset{\text{amygdalin}}{C_{20}H_{27}NO_{11}} + \underset{\text{water}}{H_2O} \rightleftarrows \underset{\substack{\text{benzoic}\\\text{aldehyde}}}{C_7H_4O} + \underset{\substack{\text{hydro-}\\\text{cyanic acid}}}{HCN} + \underset{\text{glucose}}{2(C_6H_{12}O_6)}$$

The so-called "mustard oil" is produced, along with glucose and two other compounds (see p. 398) from sinigrin, a glucoside characteristic of the mustard family. These actions are very rapid, as shown by the formation of the peculiar flavor or pungency almost as soon as the parts are crushed by the teeth and the enzyme thus brought into contact with the glucoside.

Protein enzymes. — Several enzymes are known which digest proteins. In animals their digestion proceeds by two prominent stages: first, the peptic enzymes (*i.e.* those like pepsin of the stomach) convert proteins into peptones, which are soluble and diffusible; second, the trypsin of the intestine converts proteins and peptones alike into amino-acids and other compounds, still more freely soluble and diffusible. At first protein digestion in plants was ascribed to peptic enzymes; later, because of its completeness, it was referred to tryptic enzymes and the presence of peptic enzymes was denied. Now, however, it is possible to distinguish the two classes of enzymes, though they act together and carry forward the processes to completion without a pause at any particular stage of simplification.

Inasmuch as the proteins are not prominent among surplus foods, it might seem at first sight that protein digestion was unimportant in plants. But aside from the stored food, many instances where such digestion must occur may be cited. Thus, the exhaustion of proteins to a large extent from the foliage of annuals as the seeds ripen (*e.g.* as shown in cereals), and the partial recovery of proteins from leaves of trees before their fall, presuppose protein digestion. So, also, the action of a plant parasite or saprophyte on animal bodies, and of the curious pitchers and traps of carnivorous or insectivorous plants involve protein digestion.

Assimilation. — All the digestive changes are preliminary to the translocation of foods from places of manufacture to places of storage or use, or from places of storage to places of use. And before foods are of real *use* they must be incorporated into the living substances of the body,[1] which *grows* thereby. This final step in the chemical progress of foods, by which they become a part of the living protoplasm, is known

[1] This view is only partly shared by those physiologists who believe that food can be "oxidized" directly to serve as a source of energy. See the section on Respiration (p. 403). For them the food so oxidized is no more incorporated into the body than fuel is into the furnace in which it is burnt.

as *assimilation*. To give it a name is about all that can be done at present, for until very much more is known of the chemistry of proteins, of which protoplasm chiefly consists, practically nothing can be known of the details of assimilation.

Metabolism. — The important steps in nutrition are these: (1) the making of carbohydrates in green parts properly lighted out of H_2CO_3; (2) varied modification of these and incorporation of nitrogen (often also sulfur and phosphorus) from mineral salts to form amides and finally proteins; (3) the assimilation of proteins into protoplasm. On the whole these steps are upward; the material becomes, though with many fluctuations, gradually more and more complex, until it enters upon its final, most complex, least stable, living condition. It is maintained for a time at the high level as living stuff, or it becomes a part of some more permanent portion of the body, like the cell wall; or it is broken up and reduced gradually to simpler compounds, some perhaps to be rebuilt into living matter again, some to break into simpler and simpler compounds and to leave the body (*e.g.* as CO_2, H_2, etc.).

Metabolism is an old general name for *all* the chemical changes in a living organism. The constructive phases of nutrition are often summed up in the term *anabolism* or constructive metabolism; the destructive phases as *catabolism* or destructive metabolism. In the former the processes tend to be synthetic; in the latter analytic. Having considered the synthetic processes, the analytic ones demand attention in the next chapter.

CHAPTER IV. — DESTRUCTIVE METABOLISM

1. RESPIRATION

Respiratory organs. — The word *respiration*, or its English equivalent, breathing, suggests at once the currents of air into and out of the lungs, and the bodily movements that cause them. The reason for this is that so much attention has been given to these matters in human physiology that the more important processes, which take place in the muscles and live tissues generally, have been almost ignored. This is emphasized by the fact that the phrase "respiratory organs" means the lungs and the air passages thereto, while the blood, which is an equally important adjunct to the aeration of the tissues, is not usually included. But air-passages, lungs, chest wall, diaphragm, blood vessels, and blood, not to mention others, are all necessary organs. The fundamental processes, however, take place in the living cells; and they go on there, for a time at least, whether or not, by accessory mechanical means; the oxygen of the air is supplied and the waste products removed.

Since in plants the accessory organs are very simple indeed, their structure and behavior needs little consideration, particularly as they are at the same time, in green plants, related to transpiration and to photosynthesis (see aerating system, p. 318). So botanists have focused attention upon the essential processes in respiration. This difference in emphasis has tended to obscure the fundamental likeness of this function in plants and animals.[1]

Identical in plants and animals. — Excluding the processes of aeration, respiration in plants and animals is alike in all essentials. When the likeness of the living matter in the two is considered — a likeness so great that neither microscopic observation nor analysis can distinguish them by structure, behavior, or composition — the fundamental identity is not surprising. Yet popularly it is widely believed that the respira-

[1] It has been proposed to retain the term *respiration* for the aerating processes, and to use the term *energesis* for the chemical changes in the tissues, whose end seems to be the setting free of *energy*. It remains to be seen whether or not this distinction is acceptable or important. It may prove, indeed, that the release of energy is quite incidental to other more essential processes.

tion of plants, or of green plants at least, is exactly the reverse of that of animals. This misconception is due to confusing the effect produced upon a limited volume of air by the respiration of animals and by the photosynthesis of plants, two processes which are as little comparable in their results as are walking and eating.

Neither gaseous exchange nor combustion. — The striking change that most organisms produce in the air of a limited space is the reduction in the amount of oxygen and the increase in the amount of carbon dioxid. This can readily be demonstrated by putting a considerable quantity of germinating seeds or opening flowers into a fruit jar and sealing it for a few hours. On then lowering a lighted taper into the jar, the flame will be extinguished; and a cup of baryta water will be covered quickly with a film of barium carbonate. This has led to a superficial conception of respiration, current in text-books and encyclopedias, as an exchange of the gases, oxygen and carbon dioxid, between the air and the organism. Because in the burning of wood and other carbon compounds oxygen is consumed and carbon dioxid is produced, respiration has been assumed to be a process of oxidation, in which foods undergo "combustion" in the same sense as the fuel in a furnace, the energy being liberated as heat and in other forms, when the carbon of the compounds is combined with the oxygen of the air. One striking difference between "combustion" inside an organism and outside is that the former occurs at low temperatures, while the latter takes place commonly at high temperatures. To escape this difficulty the term "physiological combustion" was invented. But the conception of respiration as an exchange of gases accompanying oxidation of carbonaceous foods is inadequate, and comparing it to any sort of combustion is more misleading than helpful.

Aerobic and anaerobic respiration. — In the first place, though ordinarily oxygen is fixed, oxygen is not indispensable to respiration; and in the second place, though ordinarily CO_2 is evolved, carbon dioxid is not a necessary product and probably in no case does the O_2 combined with the C come directly from the air. That being so, it is obvious that the above-mentioned conceptions as to respiration cannot be valid. That respiration sometimes goes on in the absence of free oxygen, makes it necessary to distinguish normal or *aerobic* respiration and intramolecular or *anaerobic* respiration.[1] Aerobic respiration proceeds only

[1] Inasmuch as under the conditions one is as really *normal* as the other, and as the term *intramolecular* expresses an interpretation of anaerobic respiration which is no

when O_2 is present in sufficient quantities, and among the end products two, CO_2 and H_2O, are characteristic, though formed in very variable quantities in proportion to the O_2 taken up. Anaerobic may replace aerobic respiration in any organism when O_2 is cut off, and may proceed for a long time; but the end products are various and quite different from those of aerobic respiration. Among them are commonly ethyl alcohol and hydrogen, and less CO_2. Certain minute organisms may pass their whole existence without oxygen, which indeed hinders or altogether stops their development, and they are thus restricted to anaerobic respiration. In most organisms, however, anaerobic respiration can be considered only as a makeshift.

Nature. — What then is the fundamental feature of a process that goes on under such different conditions and results in such diverse products? So far as now appears, respiration consists in the decomposition of the protoplasm or some of its constituent proteins, either directly, or as a result of the action of an enzyme or of some internal force (stimulus) upon it. Inasmuch as the inciting cause is rarely apparent, spontaneous or self-decomposition is often spoken of, but this merely means that the reason is unknown.

The view here presented is not the one most generally held at present, but appeals to the author as most consistent with the known facts. Many physiologists consider respiration to consist primarily in the decomposition of foods by the protoplasm or by enzymes, without their assimilation into the living substance. In this case foods are a kind of fuel for the body (see p. 406). It is not denied that some decomposition of protoplasm occurs, but this is slight; as it were, a sort of natural wear and tear in consequence of work.

Advantage. — The advantage of respiration is not certainly known, but as the plant in order to do work must expend energy, the inference is that respiration sets free energy by which that work is performed. Now complex and unstable compounds contain much available potential energy, the store of which is diminished when they decompose, and the essence of nutritive processes is the building up of those compounds which disappear in respiration. Furthermore, heat, one easily observed form of energy, is generated by respiration, though it is not known that this is of any service to the plant. But the most definite reason for connecting the release of energy with respiration is that those tissues in which growth or other work is proceeding rapidly are also characterized

longer tenable, the words *aerobic* and *anaerobic* (*aer*, air; *bios*, life; *an*, not), applied first to organisms that live in air or flourish only when it is excluded, are preferable.

by rapid respiration. This is in harmony with numberless observations in animals, in which the work can be increased at will, when a corresponding increase in the products of respiration, the consumption of nutritive materials, and the evolution of heat is readily shown. It is perhaps better to consider all those phenomena of respiration as its results, the decomposition of the protoplasm being the primary and essential feature. Indeed the phenomena of respiration may all be directed to ridding the body of the products of an inevitable decomposition of the unstable proteins of the living protoplasm.

Rôle of oxygen. — When energy is released from chemical compounds, the more completely they are decomposed the more energy is liberated, as a rule. In anaerobic respiration the decomposition does not go so far as in aerobic, for the resulting substances are not so simple, and probably therefore the energy released is far less. The fact that growth either does not occur at all, or is very limited, when oxygen is cut off from plants accustomed to it, also indicates this. Herein, indeed, appears the probable rôle of oxygen in respiration. It seems to be necessary not to combine with carbon compounds, but, by combining with and so removing substances whose presence interferes with the usual reactions, to enable the respiratory processes to go on to completion.

The common idea is that oxygen combines directly with carbon and so causes "combustion." But chemical studies of the combustion of certain gases show that it does not do this, even at high temperatures. Water vapor, which yields H and OH ions by dissociation, furnishes the necessary OH ions for facilitating the decomposition of the carbon compounds, and this decomposition does not proceed at all in the absence of water, not even in pure oxygen. The oxygen does combine, however, with hydrogen to regenerate water, so that a small quantity of water serves, provided O_2 is continually supplied. In this, O_2 behaves somewhat as the depolarizer does in a galvanic battery, wherein its function is that of an oxidizing agent to convert into water the hydrogen that otherwise would accumulate on the cathode and stop the chemical action. Undoubtedly other "depolarizers" than oxygen are present in the cells; and in some organisms the long continuance of anaerobic respiration without serious harm may be thus explicable. The presence of oxidizing enzymes, also, may be essential to the fixation of oxygen.

End products. — When, therefore, O is supplied, the end products of decomposition are in large part the most stable ones, CO_2 and H_2O. When O_2 is not available, these are less prominent, while ethyl and higher alcohols, organic acids, aromatic compounds, hydrogen, etc., are the more abundant end products. In the one case certain parts of the protoplasm break into simpler and simpler compounds; in the other the

decomposition stops while yet the materials are complex, and hydrogen appears because no oxygen is available to combine with it.

Why carbohydrates disappear. — The end products, however, probably do not represent in any case the whole of the protein molecule. Certain fragments of it, under suitable conditions, go down into CO_2 and H_2O; but others are not so far split up that they cannot be rebuilt, with necessary additions, into protein again. It seems to be the components of the protein molecule derived from carbohydrates, which are particularly liable to complete decomposition. If this nucleus alone were broken up, the ratio of free O_2 fixed to CO_2 produced should have a value of unity. This is not by any means true; the average is below 1 and the value varies from 0.3 to 5.0; so it is probable that the process is complicated by the interaction of other substances. The repair of the proteins requires chiefly carbohydrates, because the nitrogenous losses in the plant are quite inconsiderable as compared with those of an animal. So a marked effect of respiration is a disappearance of the accumulated carbohydrates.

The assumption that carbohydrates are directly decomposed in respiration rests largely on the fact that the value of the ratio $O_2 : CO_2$ is affected by the food supplied to non-green plants. Thus, in *Aspergillus* it ranges from 0.43 with 10 per cent tannin, to 1.78 with 10 per cent glucose, indicating that not composition alone but other and unknown factors are concerned. And composition, as well as these unknown factors, may produce this result indirectly, through their influence on assimilation, quite as effectively as by directly modifying the " combustion " of foods.

Loss of weight. — The transformation of carbohydrates in the repair of proteins can have little effect on the weight of the plant; but the escape of CO_2 as a gas and the evaporation of the water produced does result in a loss of weight. If the total dry weight of seeds be calculated (the percentage of water in like seeds having previously been determined), and these seeds be grown for some weeks in the dark, plants of considerable size can be raised. But on drying them, the residue will be found to weigh less than the calculated dry weight of the original seeds. This difference corresponds to the combined CO_2 and H_2O produced and lost in the course of respiration.

Production of heat. — The heat produced by respiration is often not observable at all, unless some means are used to prevent its radiation and its transfer to the air by the evaporating water. If a mass of wheat seeds be germinated, a thermometer thrust into the mass will show a temperature considerably higher than that of the air; but this is due

largely to microorganisms, whose active respiration, and especially the fermentation they cause, liberates much heat.[1] If, however, the surface of the seeds is carefully sterilized before germinating, the difference is much less, in many cases with ordinary insulation only 1–1.5° C.

By using Dewar flasks, which afford very perfect protection against loss of heat by radiation and conduction, differences of 20° C. or more have lately been found with 80 gm. of peas (weighed dry).

The opening of flowers crowded into a compact cluster within a bract, as in the calla, causes a decided rise of temperature, differences of 5–10° C. having been noted. This production of heat is continuous, though its rate varies. It is said that a kilogram of seedlings may produce heat enough per minute to warm 1 gm. of water from 0 to 50 or even 100° C. Yet under ordinary circumstances this heat is steadily dissipated.

Comparative activity. — It is commonly supposed that at best the aerobic respiration of plants is weak compared with that in animals. This is a mistake. The respiratory rate for active tissues of plants compares well, weight for weight, with that of even warm-blooded animals, and in some cases far exceeds it, if the gaseous changes may be taken as a fair measure of the process. Thus, if a man of 75 kg. produces at light work about 900 gm. CO_2 in 24 hours, the output of CO_2 equals 1.2 per cent of his weight. By the buds of lilac the output of CO_2 equals 1.8 per cent of their weight; by those of horse chestnut, 3 per cent; by seedlings of poppy, 2 per cent; by molds, 6 per cent. While a man may use in 24 hours 1 gm. of oxygen for each 100 gm. of his weight, young leaves of wheat use it at the same rate; opening flowers use 4 times as much, and some bacteria 200 times as much.

The stage of development, the general activity, and the rate of growth influence decidedly the rate of respiration. The younger and more active the tissues or organs, the more rapid, as a rule, is the respiration.

Life. — It has already been indicated that anaerobic respiration begins like aerobic, but that the decompositions cease before they attain the same extent. It may very well be, also, that they pursue a somewhat different course, on account of the lack of oxygen. Growth ordinarily ceases when growing tissues are forced to do without O_2, though some-

[1] When moist plants or manures are piled up, very high temperatures may be produced in the midst of the mass by the combined activities of many different fungi and bacteria. This "heating" may even suppress or kill off all species except those that flourish at 55–65° C.

times it continues for a time; whence it is inferred that the energy released by anaerobic respiration is usually inadequate for growth. Life, however, persists for a variable time, sometimes for weeks or months, though in active parts the functions are much disturbed after a few hours, and death shortly ensues.

2. FERMENTATION

Microorganisms. — The fact that anaerobic respiration gives rise, among other things, to alcohol and carbon dioxid, suggests at once some relation to a process long known to occur in sugary juices, like those of grapes and apples, when they are allowed to stand unsterilized and unsealed. The sugar disappears, bubbles of gas (CO_2) rise through the liquid, and considerable alcohol is formed in it. This process is known as fermentation. It was shown long ago to be due to the presence of yeast plants, for it does not occur when they are excluded. Further study has shown that analogous changes which take place in organic substances, many of them (like the souring of milk and the spoiling of meat) being familiarly known, are due to the action of other microorganisms. The application of the term *fermentation* has now been extended to cover all these changes.

Names. — Fermentations are named after the most prominent or desirable substance produced, or sometimes after the substance destroyed. Thus, the fermentation of glucose (grape sugar) is alcoholic fermentation; that of lactose (milk sugar) is lactic fermentation; that of alcohol is acetic fermentation; because alcohol, lactic acid, and acetic acid, respectively, are formed. On the contrary, the cellulose fermentation is so named because cellulose is destroyed. When proteins are attacked, evil-smelling gases are among the products, and such fermentations are frequently distinguished as putrefactions; but they are not essentially different from others. Only a few of the better known and more important fermentations can be treated here.

Alcoholic fermentation. — The alcoholic fermentation is produced in different sugars by various organisms. The sugars that are now known to be fermentable are only those the number of whose carbon atoms is 3 or a multiple of 3; thus, the trioses ($C_3H_6O_3$), hexoses ($C_6H_{12}O_6$), and nonnoses ($C_9H_{18}O_9$) are directly attacked; while the more complex carbohydrates (di- and polysaccharides), such as cane and malt sugar ($C_{12}H_{22}O_{11}$) and starch $[5n(C_6H_{10}O_5)]$, are fermented only after

they have been simplified by cleavage into hexoses. Why this limitation exists, and why within this there are others even more specific, is not known. The organisms concerned are chiefly those known as yeasts (see Saccharomycetes, p. 70), but certain molds and bacteria also give rise to ethyl alcohol, though the latter more commonly produce higher alcohols (propyl alcohol, butyl alcohol, etc.). In this connection it is to be remembered that even the higher plants produce ethyl alcohol in the course of anaerobic respiration.

The sugar is split up in large measure into CO_2 and ethyl alcohol, but there are other products, such as glycerin, succinic acid, etc., in smaller quantity. Fermentation proceeds very slowly when the yeasts are abundantly supplied with O_2; then, however, they grow and multiply rapidly, and apparently use the sugar chiefly as food. But when the supply of O_2 is small, so that their vegetative processes are hindered, fermentative action is increased. Though alcohol is produced at all times, its quantity is in a sort of inverse ratio to the favorableness of the conditions for life. When 12 per cent have accumulated in the liquid, the action is retarded, and by 14 per cent it is stopped.

Fermentation by yeasts was long believed to be due to the direct action of their protoplasm on the sugar; now it has been proved that an extract, made by grinding the yeast with sand and filtering the juice under high pressure through porcelain, can produce the same effect. The active substance, known as *zymase*, is soon destroyed, unless protected from digestion by accompanying enzymes. Similar substances have been isolated in higher plants, which are believed to act upon carbohydrates in anaerobic respiration,[1] giving rise to alcohol and CO_2 in the same proportions as in fermentation.

The economic uses of alcoholic fermentation are many. It plays a prominent rôle in the lightening of bread, in which, however, other organisms share with yeast the production of the gases that raise the dough; it is the source of commercial ethyl alcohol, which is distilled from fermented liquids, in which hexose sugars are first produced from corn and potato starch; it gives rise to the alcohol in a host of fermented liquids used as beverages: wine, beer, koumiss, pulque, saké, etc.

Lactic fermentation. — The lactic fermentation, giving rise to lactic acid, is best known in the souring of milk, and may be produced whenever lactose is present in a solution to which the lactic acid bacterium has

[1] The source of these carbohydrates is uncertain. They may be either the unassimilated carbohydrates of the food; or, equally well, a carbohydrate nucleus from the decomposition of the protoplasm.

access. As in the alcoholic fermentation, the accumulation of the products brings the action to a standstill. When 8 per cent of lactic acid has accumulated (or less in milk), the bacterium becomes inactive.

Acetic fermentation. — The acetic fermentation is due to bacteria, which oxidize ethyl and other alcohols to acids. The commonest form converts ethyl alcohol into acetic acid, $CH_3 \cdot CH_2OH + O_2 \rightleftarrows CH_3 \cdot COOH + H_2O$. In the quick process for the manufacture of vinegar, in which this fermentation is applied, dilute alcohol (6–10 per cent) is allowed to trickle over beech shavings in a deep vat, which have become covered with a slimy coating of the organisms. By the time the alcohol has reached the bottom it has been oxidized completely to acetic acid.

Butyric fermentation. — Butyric fermentation, by which butyric acid is produced from various sugars, especially lactose, and indirectly from polysaccharides, through the agency of bacteria, underlies the production of desirable flavors in butter and cheese.

Putrefactions. — The putrefaction of proteins is wrought by various bacteria, but little is known of the details. Among the numerous end products are the disagreeable gases hydrogen sulfid, mercaptans, skatol, etc.

So a multitude of fermentations might be named, each concerned with a particular compound and due to a particular organism. By the single or successive action of such organisms, complex organic matter is gradually reduced to simple forms, like those from which it was constructed, which then may enter again into the cycle and be built up, through the agency of green plants, into foods.

Advantage. — The precise rôle of fermentations in the life history of the organism that produces them is not certainly known. It is possible that they are, as respiration is supposed to be, a source of energy. The minuteness of the organisms would make possible the appropriation of this energy, even though, in contrast to that set free by respiration, it is released outside the body. From this point of view it would seem that fermentation might be considered as a substitute for respiration, though a rather ineffective one, and hence requiring an exaggerated decomposition of organic matter. On the other hand, it has been suggested that fermentation serves for the production of substances in which the producers can live, but by which other organisms are injured and so prevented from competing with them for food and room. This suggestion, however, seems forced and inadequate. Yet again, it may be

that all fermentations are effected by enzymes, as some are known to be, and that the formation of these enzymes is not so much a matter of advantage to the organism as an inevitable result of the conditions under which it develops. If this be true, to seek for explanation through advantage is a fruitless quest.

3. WASTE PRODUCTS AND ASH

Wastes not useless. — In the course of the many and varied chemical changes which take place in plants, there arise, especially in consequence of the destructive metabolism, a great number of compounds which are not usable for the building of new parts, and are not again drawn into the metabolism. Some of these are nevertheless of considerable service to the plant, and in varied ways; as, for example, in protecting it from predatory animals by disagreeable tastes or odors, in covering wounds by gummy or resinous exudations, in attracting by color or odor insects which effect pollination, etc. In spite of the usefulness of some of them, these substances are often called *waste* products, and this word may well be retained instead of the more technical term, *aplastic* products, which has been applied to them. For in every household there are like products, properly "waste," so far as the direct economy is concerned, some of which may nevertheless be collaterally serviceable.

Number. — Of the reactions by which these waste products are produced, not much is known, and they need not be considered at all here. The number of the products is very great, and it is possible to name only a few of the more important groups and examples of them. An impression of their number may be gained from the fact that in a recent work on plant chemistry more than 4000 are mentioned, and the book does not pretend to enumerate all known substances. Thus there are over 200 known alkaloids, and a single firm lists some 200 essential oils of commercial value. Yet the knowledge of the chemistry of plants is very incomplete and lags far behind that of animals.

No true excretion. — Almost all of the wastes accumulate in the tissues, for actual excretion by plants is very imperfect. Except for those which are got rid of in the fragments of bark, roots, twigs, and leaves that are shed, and the relatively minute quantities that are secreted by surface glands, or diffuse out into the water from roots and other immersed parts, there is no provision for doing more than storing these substances in some out-of-the-way place. In no case is there any ar-

rangement for continuous riddance, such as is found in the excretory organs of animals. It is also particularly noteworthy that among the wastes there are few or none except the alkaloids that contain nitrogen. Even these are not necessary products of metabolism, for the very plants that produce alkaloids most abundantly may be so grown, and healthily, as not to contain any.

Gaseous wastes. — Among gaseous wastes, the most important, CO_2 and O_2, have already been mentioned; and the water resulting from respiration, while not produced as a gas, leaves the body mostly in this form. In a few plants, notably in the stinking goosefoot and flowers of hawthorns, a very disagreeable odor makes known the escape of a gas, trimethylamin; but this is formed only in trifling amounts.

Essential oils. — Most of the odors of plants, fragrant or not, are due to the essential (volatile) oils, which are distinguishable from true oils, to which they are not at all allied chemically, by leaving only a transient spot on paper. They are especially abundant in the foliage and flowers, though there is no part but may be the seat of their production or storage. They are the more volatile constituents of complex mixtures, secreted by glands of various forms (see p. 337), whose solid residues, after the "oils" have been driven off, are resins (see below). These secretions may escape at once upon the surface, or they may be stored in intercellular receptacles and released only by crushing. In the flower leaves they are curiously distributed, being formed in the epidermis of both petals and sepals, or only in one, or only in the cells of one face, or only in lines or patches of cells. From such parts, even when in very small amounts, they may be distilled, and when more abundant they may be expressed and purified. Some are medicinal, and some are commercially valuable as perfumes for soaps, ointments, and other toilet articles. Chemically they are quite diverse; many of their constituents belong to the class of compounds known as *terpenes*.

Gums and resins. — Gums and resins occur in great variety, and often in mixtures called gum-resins and balsams. These terms are rather loosely used, and do not designate definite chemical groups. The true gums are in large part carbohydrates, arabinose being especially abundant ($C_5H_{10}O_5$), and arise from the transformation of the cell wall and growing tissues in woody plants. They swell readily in water. Gum arabic and gum tragacanth are well known commercially, and the gum of cherry and peach trees is familiar. Resins are yellowish solids, usually derivatives of essential oils, that occur dissolved in essential oils.

Thus, turpentine consists of colophony or resin dissolved in "oil of turpentine," itself a mixture of several terpenes. "Canada balsam," as used for mounting sections, consists of a resin solidified by driving off the volatile oil and redissolved in a more volatile solvent. The gum-resins or balsams are variable mixtures of gums and resins, with many other accidental constituents. The best known are asafetida, as distinguished for its disagreeable odor as are galbanum, myrrh, and frankincense, the chief components of incense from time immemorial, for their fragrant smoke. They exude from wounds in various oriental shrubs and solidify in drops and irregular masses.

Organic acids. — The organic acids are also numerous, but four predominate. These four, oxalic, malic, tartaric, and citric acids, are all very widely distributed and are not infrequently associated. *Oxalic acid* ($COOH \cdot COOH$) is not certainly known to occur in the free state, but is abundant in salts of calcium, potassium-hydrogen, and magnesium. Calcium oxalate is found in every large group of plants except bryophytes. It crystallizes in long slender needles (raphides) or as "crystal sand," with two molecules of water; or it forms large single crystals or crystal aggregates, of octahedral form, when it combines with six molecules of water. (See Part III, fig. 919.) Magnesium oxalate forms spherites. *Malic acid* ($COOH \cdot CH_2 \cdot CHOH \cdot COOH$), which is almost as widely distributed as oxalic, occurs in the juice of many unripe fruits, especially the apple, pear, cherry, etc., either free or in salts of calcium and potassium. *Tartaric acid* ($COOH \cdot CHOH \cdot CHOH \cdot COOH$) is closely allied to malic acid. It is found abundantly in the juice of grapes as potassium-hydrogen tartrate. *Citric acid* $\left\{ OH \cdot \begin{matrix} CH_2 \cdot COOH \\ C \cdot COOH \\ CH_2 \cdot COOH \end{matrix} \right\}$ occurs in the juice of many plants, being especially abundant in the fruits of the citrus family (lemon, lime, orange, etc.).

Tannins. — The tannins are numerous and widely distributed, occurring especially in bark, wood, leaves, fruits, and galls. They are bitter and astringent substances, which form insoluble compounds with proteins and gelatin, and so are used for converting hides into leather. Tea leaves contain 14–16 per cent or more (dry weight), various barks up to 40 per cent, and galls up to 60 per cent. Some substances included in the loose term *tannins* are glucosides, and such as can be made to yield glucose by digestion may be considered as plastic substances rather than wastes.

Alkaloids. — The alkaloids are numerous, and very important medicinally, as they are dangerous poisons or useful local stimulants, according to circumstances. A few, such as *caffein* from tea and coffee, *theobromin* from the seeds of cacao ("cocoa"), and the deadly *muscarin* from the poisonous mushroom (*Amanita muscaria*), are not related to the alkaloids proper, which are for the most part derivatives of pyridin and chinolin. The true alkaloids are found in fungi and various seed plants, but are most common in certain families of dicotyls. For example, in the Papaveraceae, the oriental poppy alone yields more than twenty alkaloids, of which *morphin*, *narcotin*, and *codein* are best known; in the Solanaceae, tobacco contains *nicotin* and others, and most of the other genera yield *atropin* and a number allied to it; a great number of the Apocynaceae have alkaloids in their latex, at least twenty different ones being known; in the Rubiaceae, the cinchonas and their allies produce more than thirty alkaloids, of which *quinin* and *cinchonin* are widely known; in the Loganiaceae, seeds of *Strychnos nux-vomica* yield *strychnin* and *brucin*, while another species yields several "*curare*" alkaloids; and in the Erythroxylaceae, coca yields among others *cocain*, at once highly useful as a local anesthetic and utterly destructive to body and mind when used habitually.

Coloring matters of flowers, fruits, barks, seeds, etc., are too numerous and varied to be discussed here.

Ash. — Mineral salts are present, sometimes amorphous, incrusting or incorporated in the cell walls, as is the case with silica; sometimes crystallized, as is the case with calcium oxalate. The ash of plants consists of the total mineral matter left as oxids when completely burned. Analysis shows that the amount and content of the ash varies much in the same plant in different situations, thus indicating that in part (and doubtless in large part) these materials are determined not by the "needs" of the plant but by the solutions which have opportunity to wander into it. Cultures under special conditions have shown that plants may be deprived of many of the chemical elements ordinarily found, and no evil effects follow; but the absence of others has obvious ill effects. Thus silica is an abundant material in the cell walls of the epidermis of most cereals; yet corn has been cultivated through four generations with practically no silica.

Necessary elements. — A list of the elements that have been found in the ash of one plant or another would be almost a list of the commoner

elements themselves, over thirty out of the present total of seventy-eight having been recorded. Yet of this large number only a few seem to be indispensable. These are usually reckoned as calcium, potassium, magnesium, and iron; while chlorin and sodium are present in all and may be necessary. Many attempts have been made to determine the precise rôle of each of these indispensable elements, with rather conflicting results. It does not seem possible by cultures which omit a particular element to reach reliable conclusions; nor is it at all likely that the rôle of any particular element is simple, and the withdrawal of one may permit others to act in a wholly different way. Thus if plants be grown in solutions of calcium chlorid or of magnesium chlorid of a certain concentration, they will die; but if the two be mixed in the same concentration, the plants will grow well. Singly both are injurious, together they are not, though no reaction occurs between them.

When therefore it is said that a definite amount of each "indispensable" element is needed by a plant, and that the minimum determines the crop ("law of the minimum"); that on potassium depends the formation of new organs at the growing point; that calcium is required for the transfer of starch, and so on, all such statements must be considered as extremely doubtful and liable to complete reversal when a deeper insight is gained into the processes concerned.

CHAPTER V. — GROWTH AND MOVEMENT

1. GROWTH

Ideas involved. — Nothing about plants as a whole is more readily seen than that they grow, and in due course unfold new organs. However small and simple, however large and complex, growth is almost always obvious, and sometimes it becomes striking because of its rapidity or its long duration. Two ideas are involved in the term *growth* as ordinarily used, (*a*) an increase in size and (*b*) the formation of new organs. The latter is sometimes distinguished under the term *development*, and if one speaks of growth and development, the term *growth* must be limited to the enlargement of already formed cells. But the terms are nearly synonymous; though growth may be restricted for a time to cells already formed, it normally leads to the formation of new organs; and though development is possible without enlargement, it is usually accompanied by an increase in size. The production of new organic material is not essential; when the corn seedling, raised in the dark, grows into a plant many times larger, the stored organic material has been merely rearranged, with the addition of water, and when the surplus food has been fully used for growth, there is actually a smaller total of dry matter than when growth began. Additional organic matter can be produced only when the conditions for photosynthesis are fulfilled.

Few plants have so definite a cycle of development as most animals. In some cases leaves produced in the juvenile period differ from those of later stages.[1] Again, leaves developed at certain periods are so different in form and texture as to be really different organs, as in the case of bud scales, floral parts, etc. But these periods of flowering or seed formation or other reproductive process are determined largely by external conditions, and little or not at all by the fact that the plant has reached a certain stage of maturity, though of course the formation of the special organs, as of all others, is conditioned by the supply of constructive

[1] These juvenile forms, however, may appear later under suitable conditions. See Part III, p. 596.

material. Plants, therefore, do not in general have a definite stage of maturity, and a corresponding form. They do have, however, periods characterized by growth, including the formation of new organs and their development. These periods occur once, being limited to a single season or less, as in the case of annuals; or twice, as in biennials; or they are repeated, season after season, as in perennials. This periodicity is less marked in equable tropical climates, but is rarely, if ever, entirely absent.

Phases. — If the history of any limited portion of a plant be followed (and the more limited the better, even to a single cell), it can be observed to pass through a development in which may be recognized three phases. The first phase may be called the formative phase; the second, the phase of enlargement; and the third the phase of maturation. These phases are characterized clearly enough by certain peculiarities of structure and behavior, but they are not sharply delimited. On the contrary, the first passes by imperceptible gradations into the second, and the second into the third; then growth finally ceases, unless some unusual stimulus brings the cells again into an active state.

Formative phase. — The formative phase is the earliest. Every plant begins its existence as a single cell, and even when this one has increased to many, they usually remain practically alike. The embryo in seed plants, at the time when it resumes its interrupted growth, usually consists of cells all in the formative stage. They are characterized by a relatively large nucleus, abundant cytoplasm with only minute vacuoles, and thin walls. In this phase the frequent division of the cells is a feature, and in consequence of the more rapid production of new cells by division at certain points, the primordia of new organs appear (fig. 666). Some of the simpler plants never get beyond this phase, except as to their reproductive organs. Even in the larger plants, some of the cells permanently retain these characters, and so constitute formative centers or growing points; but far the greater number pass gradually into the second phase and the third, assuming quite a different aspect and behavior. In particular, the power of division is given up.

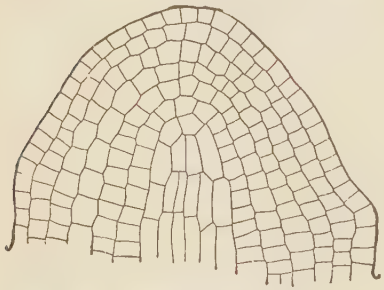


Fig. 666. — Growing point of *Hippuris*. — After De Bary.

Primary meristem. — The formative regions in thallophytes are often rather indefinite, with a tendency in the higher forms to be restricted to the apex of the body. In the bryophytes they are found only at the apex, while in the vascular plants they persist commonly at both apex and base, *i.e.* at the tip of each axis and of each root. Here the active division of the formative cells and the differentiation of their progeny adds to the length of the body at one or both ends. There may be a single cell acting as the source of all, as in ferns, or a group of initials, as in seed plants (fig. 666). The repeated division of these initials and their progeny being the important feature, the formative tissue is designated as *meristem*, and because this meristem persists from the earliest stage in the life history, it is the *primary* meristem.

Secondary meristem. — Regularly in certain regions and accidentally in others, tissues that have passed beyond the formative phase regain the power of division and exercise it for a longer or shorter time. Thus, in all plants whose xylem and phloem bundles show secondary thickening, a layer of cells between the two becomes a *secondary meristem* (cambium), and these initials may produce new cells on either face or both, which are gradually transformed into elements like their neighbors, while the initials continue to divide through the season, or function year after year. Again, a certain zone of the cortex or even the epidermis itself may resume active division, becoming a secondary meristem called the *phellogen*, whose offspring, the suberized *periderm*, constitutes a layer of cork protecting the surface (see fig. 539). Wounds, the presence of a parasite, or other stimuli may call again into active division almost any live cells, and the resulting tissues will cover the wound with a *callus*, or produce the deformity characteristic of the particular injury or parasite.

Origin of branches. — In the primary meristem of the stem the primordia of new organs are produced at the surface, the first indication of a new lateral branch, whether a shoot or a leaf, being a slight elevation of the surface, due to more rapid growth of cells at that point. This mode of origin is known as *exogenous* (fig. 666) and is characteristic of branches of the shoot axis. In the root, on the contrary, the first appearance of a lateral branch is not at the surface, nor in the primary meristem, but at the limit of the stele or central cylinder (within the cortex), and among cells which have given over for a time active division and growth (fig. 667). The new branch must break through the cortex, since it is *endogenous* in origin; and this is characteristic of the root axis. Adventitious growing points, giving rise to new shoots, may appear in

this endogenous fashion upon roots, and likewise on old shoots or leaves. They commonly owe their origin to some external stimulus (see p. 428). Many of the growing points that are formed regularly (exogenously) on the shoot do not develop, for one reason or another. They may then be overgrown completely in woody plants, and so lie dormant for years, to be called into activity when some accident has checked the growth of others, formerly more favorably situated. Not every shoot, then, that appears to come from the interior is really endogenous in origin.

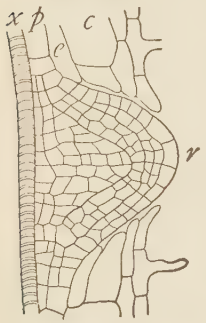


FIG. 667. — Endogenous origin of a lateral root (*r*) of ice plant (*Mesembryanthemun crystallinum*): *c*, primary cortex, and *e*, endodermis, ruptured by young root; *p*, pericycle, from which it arises; *x*, primary xylem element. — After VAN TIEGHEM and DOULIOT.

Phase of enlargement. — As cells newly formed in the meristem grow older, they enter gradually upon the second phase of development. This is characterized by enlargement, oftentimes so great and so rapid as to be very remarkable. In this period the volume of the cell not infrequently increases a thousandfold or more, though ordinarily much less. Of course this involves rapid growth of the cell wall in area, and if the cytoplasm were relatively as abundant as in the earliest stage, it would require the formation of a large mass of costly material. But while the cytoplasm does actually increase considerably, much the greater part of the cell is occupied by the water which enters it. Hence an indispensable condition for growth is an adequate supply of water; and the dwarfing which results from a deficiency of water is partly a direct consequence of the non-distension of the cells in this stage. The water enters the protoplasm, doubtless as a result of the formation of substances having a high osmotic pressure. It enlarges the minute vacuoles everywhere through the cytoplasm, until some become so distended as to merge, forming fewer but larger ones. This process continues until in the center a few large vacuoles, or often only one, occupy the greater part of the space, while the major portion of the cytoplasm lies next the cell wall as a relatively thin layer, containing the nucleus, plastids, and other inclusions (see diagram, fig. 619). It will be apparent that since this many-fold enlargement is attained so largely at the expense of water, plant growth is relatively economical.

Unequal enlargement. — The young cell has its three dimensions nearly equal. Enlargement takes place in all dimensions, but to different

degrees, according to circumstances. Thus, cells which are part of an elongated organ like a stem, are likely to grow much more in the longitudinal diameter than the transverse. The real reason for these inequalities of growth is obscure. To say that they are due to "inherent causes" or are determined by "heredity" in no wise enlightens the inquirer. In a few cases they are referable to definite agencies. Thus, the cells near the upper surface of a leaf are influenced, mainly by light, to grow longer in the axis at right angles to the surface than in the other two.[1] The sum total of growth in the individual cells determines in large measure the final form of the organ in which they lie. In most cases the causes which determine the general course of growth can be analyzed at present as little as those which determine the form of the single cell; but the effect of external agents is often detected, and in many cases it is dominant (see section 3, p. 435).

Grand period. — Enlargement proceeds at an unequal pace, even though the external conditions which affect the rate are kept uniform. In the earlier portion of the period it is slow, then it becomes more and more rapid until it attains a maximum, when it quickly falls off and gradually comes to an end. If the progress is graphically represented by plotting the increment from day to day, a curve is obtained of which fig. 668 is an example. This is the history, indeed, of the growth in length of a short portion of a stem, which is made up of a multitude of cells in the phase of enlargement. In a similar way the growth in volume of a fruit, such as an apple or a pumpkin, might be described. The total period of enlargement is named the *grand period* of growth, to distinguish it from periodic variations in the rate within the grand period, some of which are due to periodically acting external agents, such as light and heat (daily period, see p. 436), and others to causes unknown and hence called "spontaneous" variations.

The same features of the course of growth may be seen when the increment of successive small portions of an axis is recorded. Thus if a root is marked into millimeter spaces, or a stem into longer spaces and the increment of each is recorded for a number of hours, it will appear that certain spaces are growing more rapidly than others, respectively more or less distant from the tip, *i.e.* older or younger.

The increment in twenty-four hours of each of ten 1 mm. spaces of a root of *Vicia* is here shown:

I	II	III	IV	V	VI	VII	VIII	IX	X
1.5	5.8	8.2	3.5	1.6	1.3	0.5	0.3	0.2	0.1

[1] Transpiration may be another factor; the precise relation of the two is uncertain. See Part III, p. 536.

Similarly the increase in forty hours of twelve 3.5 mm. spaces of a stem of *Phaseolus:*

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
2	2.5	4.5	**6.5**	5.5	3.0	1.8	1.0	1.0	0.5	0.5	0.5

Inspection of these records shows that the two younger millimeters of the root and the seven older are growing less rapidly than the third; in the stem the fourteenth to the seventeenth millimeters (space IV) are growing most rapidly, and beyond this the older a division is the more slowly it grows.

Growing regions. — Comparison of the total length of root and stem still growing appreciably shows a striking difference. About 1 cm.

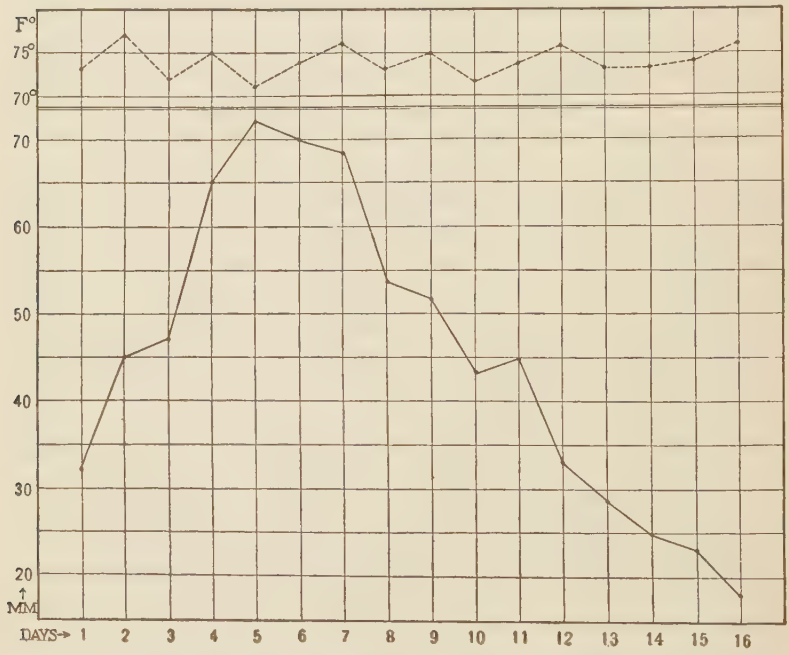


FIG. 668. — Grand curve of growth (solid line): the first day of the observation was evidently after fairly rapid growth had begun; it attained a maximum on the fifth day, with an increment of 72 mm.; thence the rate falls off rapidly, and on the sixteenth day is only 18 mm.; growth rate magnified 10 times. The temperature curve (broken line) for the same days runs between 71 and 77° F. — From data by SPOEHR.

of the root and more than 4 cm. of the stem is shown to be growing by the record above. In general the total elongating portion of a root scarcely exceeds this; but in many stems 10–20 cm. are found elongating, and in twining plants 40–60 or even 80 cm. may be growing.

The growth of aerial stems is not hindered by the medium. When they grow underground, the apex is protected by a cluster of overarching scales. Growth of such stems is seldom rapid, but when it is, as in the extensive running rootstocks of couch grass, the terminal bud is sharp-pointed and smooth, so that it offers the least resistance to being driven through the soil; at the same time the firm scales protect the primary meristem behind. In the root it is obviously advantageous to have the growth zone restricted, and to have the zone of most rapid growth as near the apex as possible; for, so much as any part behind it elongates, so far is the tip actually driven through the soil. The sloughing and slimy surface of the root cap lubricates the advancing apex, thus facilitating its passage. For good growth of roots (which makes for good growth above also), it is desirable that the soil have an optimum content of water, since it has been shown that its resistance to penetration is then at a minimum. Drought, indeed, hinders root growth doubly; it not only retards enlargement directly by lack of water, but also, by compacting most soils, mechanically opposes the extension of the root system, and so intensifies the difficulty of procuring the necessary water.

Nutations. — The rate of elongation is not only different in different sections *along* the axis; it is also unequal in different segments *around* the axis. This is especially marked in bilateral organs, such as leaves, and varies from one face to another at different periods of development. Thus, most leaves when young grow more rapidly on the back (later the under surface), so that they are appressed to the stem; or they arch over its apex when they outgrow it, as they commonly do, forming a " bud " there. Later, growth becomes more rapid on the inner face (at maturity the upper surface) and the bud opens. Local differences in rate lead to the folding and rolling so characteristic of young leaves in the bud. In radially symmetrical organs, such as stems, inequality of growth on different radii leads to bending, so that the tip is not erect but more or less declined. As the most rapid growth shifts to different segments around the axis, the tip nods successively to all points of the compass, and so describes a very irregular ellipse or circle, or, considering also its upward growth, a very irregular ascending spiral. Plotting successive observations on a plane shows tracings like fig. 669. The nodding of leaves or stems or roots on account of unequal growth is called *nutation*. The inequalities in the rate of growth may be due to unknown causes, assumed to be internal, when the corresponding nutation is called spontaneous or autonomic; or they may be due to external causes (stimuli),

when the nutations are said to be induced. The latter will be particularly discussed later (see section 4, p. 442, and section 7, p. 458).

Rapidity. — The absolute rate of growth in the period of enlargement is, of course, extremely different in different plants and under different conditions. A few cases may give an idea of the upper limits. The filaments of wheat stamens at the time of blooming grow for a brief time at the rate of 1.8 mm. per minute, which is about the rate at which the minute hand of a man's watch travels. If such a rate continued for 24 hours, they would become 2.5 m. long. The leaf sheath of the banana grows at the rate of 1.1 mm. and that of bamboo 0.6 mm. per minute. When the century-plant blooms (as it does in 10–25 years), a shaft about 15 mm. in diameter rises to a height of 6–8 m. at the rate of about 15 cm. per day.

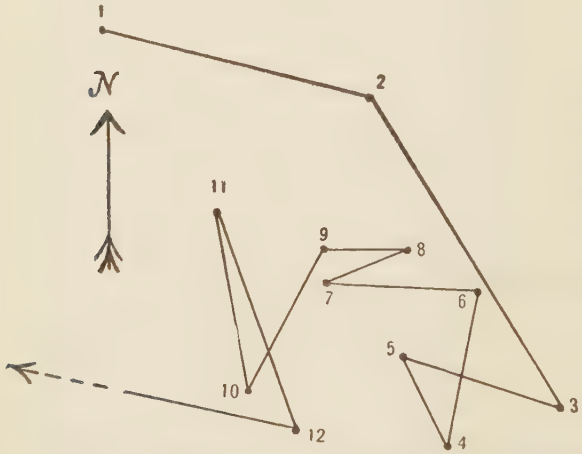


FIG. 669. — Nutations of a young sunflower plant: *1* position at 9 A.M., *2* 9:15, *3* 9:30, *4* 9:45, *5* 10:00, *6* 10:15, *7* 10:30, *8* 11:00, *9* 11:30, *10* 12 M., *11* 1:00 P.M., *12* 2:00; from point *12* the plant made a deep nod to the west till 4 P.M., then again eastward till 5:00, again westward till 6:00, and finally to original meridian at 9:00 P.M. — From data by LAND.

Phase of maturation. — The phase of maturation is the final phase of growth. This phase is entered upon only when enlargement has practically ceased; therefore its progress is not measurable, though it is quite as important as the preceding. During this phase the cells attain their mature form and character. In all cases the thickening of the cell wall is obvious, though often slight; but sometimes it proceeds to such an extreme as to be the most notable change. The thickening is never uniform, and sometimes thin and thicker spots in patterns produce an effect of sculpturing that is characteristic, as in the tracheae and tracheids (figs. 640, 641). Conversely the resorption of certain parts of the wall may occur, as the end partitions of sieve tubes and of the components of

tracheae and the thin portions of the wall in the scalariform tracheids of ferns. In case great thickening occurs, the death of the protoplast is likely to follow, and this is regularly the case in tracheary tissue. When that occurs, further modification of the wall is possible only by the agency of adjacent live cells, by chemical reaction in the wall substances, or by mere impregnation with solutes which may be precipitated or absorbed. So proceed such changes as the coloring and other alterations which mark the heart wood of trees.

Tension of tissues. — When growth is finally at an end in any region, it is found that the various tissues have not grown equally. Hence there exist strains or tensions; one region is compressed, another is stretched. These inequalities tend to adjust themselves if the regions are parted artificially, as when the pith, the bark, and the wood are separated from one another. Similarly, tensions due to unequal turgor exist (see p. 310). All these strains acting in different directions within the structure tend to increase its rigidity, just as do like strains in a latticed girder or a bridge truss.

Conditions. — The conditions for growth are first of all an adequate supply of water, for unless turgor of a meristem region is maintained, division of the cells is impossible, and unless an adequate amount of water be present, enlargement of formed cells is limited. Secondly, there must be a sufficient supply of constructive materials; for though water plays an extraordinary part in enlargement, there is needed much food for making new cytoplasm as new cells arise by division and enlarge. Nuclear material, cell-wall stuff, and much besides must be steadily constructed by the protoplasts, and the growing region is therefore the seat of intense chemical activity. Thirdly, oxygen is necessary, probably to permit the metabolism in general, and especially the respiratory changes, to proceed properly. For though growth has been observed in the absence of oxygen, it is quite limited, and, having been detected only by measurement, was probably due solely to the distention by water. Cell division also is checked by lack of O_2. Lastly, growth, like all other phenomena, goes on only within certain limits of temperature, other conditions being suitable. The optimum (different for different plants and for the same plant under different conditions) usually lies between 25° and 32° C., and the extremes are near 0° and 42° C. Any one of the conditions named may likewise vary within rather wide limits, and any one being unfavorable may retard or stop growth. Yet when all the conditions are favorable, periodic

variations still mark the rate of growth, indicating clearly that there are unknown factors that operate with or against the known factors to affect it. The existence of such unknown influences is further shown by the fact that growth ceases, sooner or later, in individual cells, and often in the whole plant, in spite of all efforts to supply appropriate conditions.

External agents. — A study of growth shows that external agents produce obvious effects. They do, indeed, affect every function, and much investigation is still necessary before the full extent of their influence is known. But growth is at once so fundamental and so easy to observe, that it affords the best means for showing how extraordinary a part external agents play in determining the form and behavior of plants. To this phase of plant life attention must now be directed.

2. IRRITABILITY

External agents. — It is a matter of common observation that the size and form of plants is affected by the conditions under which they are grown. The luxuriance of weeds in a neglected garden, in contrast with their stunted forms on a dry roadside; the rich green corn of a high prairie, in contrast with the yellowish and starved plants on a wet clay field; the thrifty trees of a park, in contrast with the struggling and dying ones along a paved street, can hardly fail of notice by the most unobservant. These differences show clearly that the complex of conditions external to the plant profoundly affects its internal processes. As all functions center in the living stuff, protoplasm, the conclusion is that protoplasm is *sensitive* to the various agents that act upon it (or *irritable*); that is, that it *reacts* or *responds* to these by altering its behavior in some way. In that event the agent producing the reaction is a *stimulus*. These three topics, stimulus, response, and sensitiveness or excitability, require consideration.

Variety of stimuli. — The forces that act upon any plant are many, and varied in direction and intensity; and their combinations are almost infinite. Consider a tree, growing in a Chicago park. Every day the light which falls on it varies both in direction and in intensity from hour to hour, and is almost lacking at night; furthermore it varies from day to day and season to season. The temperature is hardly the same from one hour to another, and in this climate occasionally changes 10° C. within twice as many minutes, while the seasonal changes range

over some 70° C. The humidity of the air shows like hourly, daily, and seasonal fluctuations, and the tree may be thrashed by a parching wind or wrapped in a dripping fog. A gentle shower, torrential rain, or hail may fall upon it within the hour; and with a change of season it may be weighed down by sleet and snow. The underground parts suffer less extreme variations of temperature than the top. The water content of the soil swings from the drought of summer to the saturation of late winter and spring, and the solutes vary more or less in concentration with the rains and evaporation. Combine all these in as many ways as possible, and some idea is obtained of the variations in external conditions which may affect the plant.

Adjustment.[1] — To many of these a plant must be able to adjust itself on pain of death, and suitable response to others is advantageous. The plant is indeed a self-adjusting[1] mechanism, whose reactions are oftentimes more delicate than those of our own bodies, with all their special senses and complicated sense organs. Thus, many a tendril is sensitive to a mechanical stimulus which we cannot perceive, even by the tip of the tongue, the portion of the body most sensitive to contact; and some plants distinguish differences of illumination which are inappreciable to the eye. On the whole, it is perhaps fair to say that plants are more responsive than animals. The plant has mostly to take what comes and make the best of it; the animal often takes shelter from unfavorable conditions or migrates to a gentler climate.

Intricate relations. — It is extremely difficult to disentangle the complex of forces acting on a plant and to assign to each its special influence. Out of them all only a few have yet been isolated. What are known as general or formative stimuli, namely, the totality of physical conditions, external and internal, which determine the general course of development and consequently the form of the plant as a whole or of any particular organ, furnish especially intricate problems, because it is so difficult to alter only one condition experimentally, or to evaluate the influence of those which cannot be controlled. Experience is showing, too, that so-called special stimuli, *i.e.* those which act locally, such as gravity, light, heat, etc., are interrelated, and their effects are unexpectedly interwoven. No phase of plant life requires more careful experimentation and more caution in inference than the study of stimuli and the responses to them.

[1] This term must be understood as if it were applied to a steam engine or a dynamo, both of which adjust themselves automatically to their "load."

Definition. — A stimulus is any change in the intensity or direction of application of energy which produces an appreciable effect upon living protoplasts. Of course when no appreciable effect is produced, the energy may differ neither in amount nor form from that which does arouse a reaction; and effects may be produced which are not perceived because improper tests are applied. A stimulus, thus, has no absolute value; it implies not a definite amount of energy measured in physical units, but merely enough applied suddenly enough to call forth a reaction as revealed by some arbitrary test. Therefore, what is a stimulus under certain conditions, is not a stimulus under others.[1] Nor need the stimulus arise or act outside the plant as a whole. It may originate in one part and act upon an adjacent part, even in one protoplast and act upon another. These stimuli, in one sense external and in another internal, are most difficult to study. They are in part, and perhaps wholly, the occasion for the reactions that are called autonomic, or less properly "spontaneous."

Kinds. — Stimuli may be classified for convenience as mechanical, chemical, and ethereal. Under mechanical stimuli are grouped those which depend upon mass movements, resulting in contact, impact, friction, pressure, etc., upon the plant. For lack of definite knowledge of the nature of gravitation, the stimulus of gravity may be conveniently included here, since it depends upon mass attraction and induces mass movements. Under chemical stimuli are included those whose action depends on their chemical quality — their composition and molecular structure — rather than on their mass. Ethereal stimuli comprise those propagated as vibrations in the ether and distinguished according to the length of the waves as light, heat, and electricity.

Modes of reaction. — The action of a stimulus results in stimulation or excitation, and this may or may not lead to an observable reaction, depending upon the state of the protoplasm and the means used to detect a change in its behavior. Thus, immediately upon excitation a change in the electrical condition of the protoplast occurs, but this does not manifest itself to our senses, unless the stimulated region and an unstimulated one are put into electrical connection with the poles of a sensitive galvanometer (fig. 670). At the same moment a contraction of the proto-

[1] No sharp distinction can be drawn between the stimuli which are followed by a prompt and easily observable response and those external agents whose very gradual change has no early apparent effect, but produces ultimately some deviation from the usual course of development. In the broad sense both are stimuli, but the term is usually applied only to the former, in which sense it is here defined.

plasts occurs, and this may or may not be apparent. It expresses itself by a change of position in the leaf of *Biophytum* (fig. 670), or of *Mimosa* because there is at the base of the leaf a cushion of cells, whose lower ones, on account of the stimulation, exude some of the water that kept them tense more readily than do the upper ones. Again, upon stimulation there may be a change in the rate or amount of some function or, more rarely, a change in the character of a function. Thus, the protoplasm of a gland may be caused to secrete more or less rapidly than before, or the protoplasm in a growing cell may have its growth accelerated or retarded. Further, a gland may have the character of its

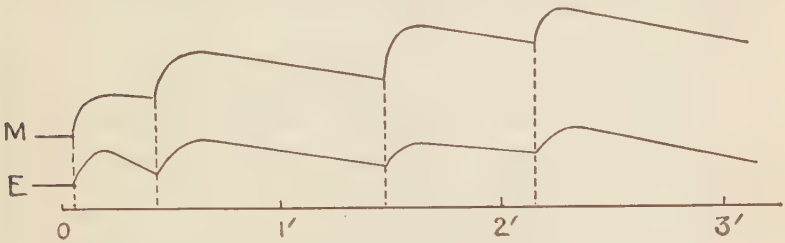


FIG. 670. — Records of simultaneous mechanical (*M*) and electrical (*E*) response in *Biophytum:* the figures are seconds; dotted lines show the moment of application of a stimulus, and the solid lines the deflection of the leaflet or of the galvanometer needle. — After BOSE.

secretion profoundly altered by excitation, or a part not growing may have its cells set again into active division and growth.

Sensitive plants. — The fact that certain plants, having a special mechanism, respond to a stimulus quickly by a mechanical movement has given them an undeserved reputation as "sensitive plants" *par excellence;* but they are not really more sensitive than others. Whether a plant exhibits movements or not depends on whether it has an appropriate mechanism to permit the protoplasmic contractions to propel it through the water, or the changed turgor to displace an organ, or the changed rate of growth to cause a curvature. Movements, then, are favorable for a study of sensitiveness merely because they are obvious reactions that can often be observed without apparatus. They do not signify unusual sensitiveness, nor does immobility imply its lack. *Every plant responds appropriately to a sufficient stimulus, and every plant is therefore a sensitive plant.*

Propagation of the excitation. — The reaction specially observed is not usually the only one. It may be only one of a series, and curvature,

resulting in movement, is most likely to be merely the *end* reaction. Thus if a primary root of a bean be set horizontal, the first reaction occurs instantly and in the very tip of the root, but it is not visible; only after a half an hour or more, at a distance of 2–3 mm. from the tip, does a growth reaction set in that starts to turn the root tip downward. Between the first reaction and the last there must have been a series of changes, each of which was a reaction to a preceding stimulus and a stimulus to a succeeding reaction. By a rough analogy the process may be compared to the tumbling of a row of blocks, each falling by reason of the impulse from its predecessor and impelling its successor to fall. The push that displaced the first one is the primary stimulus, and if the last were properly connected mechanically, it might, for the end reaction, ring a bell or fire a gun. Such a series of reactions is often spoken of as the transmission of the stimulus. More properly it is the propagation of the excitation. It is equally the propagation of a reaction.

None of these phrases nor the above analogy should be understood to require that the reactions in a series are necessarily alike, nor is the end reaction the only one to which the term properly belongs, though it is usually so applied unless the contrary is indicated.

Perceptive region. — The region where the first reaction occurs is often called the receptive or perceptive [1] region, particularly if a later and obvious end reaction occurs at another place. Since in animals a similar localization of sensitiveness for special stimuli marks the peripheral portion of sense organs, these regions in plants, especially when very circumscribed, may be looked upon as sensory organs of the simplest sort.[2] Regions of this sort, sensitive to gravity and light as stimuli, will be described later (pp. 463, 477). In the great majority of cases, however, perception is not strictly localized, and the condition resembles rather that in the diffuse senses of animals, like those of touch and temperature.

Transmission. — Special tracts, the nerves, exist in almost all animals, along which the excitation is propagated, but nothing at all comparable has been found in plants, though this claim has been made more than once. The most that can be said is that propagation is more rapid lengthwise than crosswise of the cells of a tissue and in some tissues is easier than in others. Presumably the propagation is from protoplast to protoplast by way of the slender threads that connect them, traversing

[1] These words are used in a figurative sense, and the last must not be understood to have its usual psychological implication.

[2] Here again it is necessary to point out that in no sense is consciousness implied.

the walls. It is not at all certain that there are not other more mechanical means of transmitting the disturbance that eventuates in movement.[1]

Responsive region. — Corresponding to the perceptive region, the place where the final reaction occurs is called the active or responsive region. Of course it is not more active or responsive than the intervening regions; but attention is fixed on it as the seat of the selected reaction. Thus, in the root above referred to, the perceptive region is in the root cap, the excitation is propagated backwards through several millimeters of meristematic cells to those in the phase of enlargement, and the region of most rapid growth is the responsive region, because there the growth rate is unequally affected on the upper and under side, and so a curvature appears in that zone, which turns the tip downward again.

Mechanism of reaction. — Consideration of even one such curvature shows that the nature of the reaction is in no way determined by the nature of the stimulus, since the same stimulus produces a number of reactions differing entirely from the end reaction, curvature. When many movements are studied, this feature appears most strikingly, for it is seen that the same stimulus may produce curvatures in exactly opposite directions in different parts, such as a root and a shoot, while different stimuli may call forth identical responses. Further, stimuli of the same sort at different intensities may call forth opposite reactions. The mode of action is determined in fact by the mechanism concerned. Just as an electric current may ring a doorbell, start an engine, or explode a mine, according to the mechanism at the end of the wire; so an electric current may shorten a stamen, drop a leaf, or curve a tendril, according to the mechanism set into operation in the plant. Yet probably there is some effect, fundamentally similar in each case, which works out to a different final result, just as, in the comparison, the magnetizing of an iron bar underlies the varied results.

Tropic, nastic, taxic movements. — In some cases, however, the stimulus in a measure controls the reaction. A stimulus that acts upon plants from a definite direction, and consequently from one side, may determine by that fact the plane of the consequent curvature, provided the organ be physiologically radial, *i.e.* capable of response in any plane.

[1] The "nerves" of leaves are so called only by analogy, as the correlative terms, "veins" and "ribs," indicate. They probably have nothing to do with transmitting an excitation in ordinary cases, though some recent observations allege the contrary.

Such curvatures are called in general *tropic* and the phenomena *tropisms*. To these terms is often prefixed a word indicating the stimulus which calls forth the tropism, as geotropism (*gē*, the earth = gravity), phototropism (*photos*, light), etc. (see p. 458). When a curvature evoked by either a uniform or a one-sided stimulus is restricted to a single plane by the bifacial structure of the organ, the curvatures are called *nastic*, and the phenomena *nasties*. This term is also applied to like curvatures due to unknown ("internal" or "inherent") causes. Thus we have epinasty and hyponasty, photonasty, photepinasty, etc. (see further, p. 442). In the organisms capable of locomotion, a one-sided stimulus may determine the direction of creeping or swimming. These phenomena are *taxic*, collectively *taxies*, and individually chemotaxy, phototaxy, geotaxy, etc., according to the stimulus (see p. 446).

Energy relations. — Not only is the mode of reaction independent of the kind of stimulus, but its energy is disproportionate to the amount of energy expended in excitation. The stimulus, therefore, cannot be the sole cause of the reaction, though the two stand related to each other apparently as cause and effect. On the unexpected pricking of the finger, little energy is expended; the sudden jerking away of the hand involves many times as much. Somewhere this energy must have been released and applied; and this is one reaction of the series, whose final one was movement. So in the plant, stimulation often involves a mere fraction of the energy expended in the final movement; it is released, presumably from the protoplasm or some part of it that is particularly unstable, and is applied to the work. If this be so, the chemical changes (metabolism) ought to be different in a stimulated and unstimulated organ.

This hypothesis, however, has not yet been verified experimentally. Reinvestigation of the one case in which such a result was reported has produced a conflict of evidence.

Another hypothesis, that stimulation results in molecular strain only, from which there is gradual recovery, sufficiently accounts for fatigue (see next paragraph), but does not account for the disparity in energy between stimulus and reaction, the existence of which its advocates merely ignore or deny.

Fatigue, tetanus, and summation. — After an organ is stimulated once and the response occurs, the original state is presently regained, and the organ is ready to respond again as at first (fig. 671). If several stimuli follow, each before complete recovery, the responses are of less extent than before. This effect is described by the term *fatigue*, and in many cases the responses gradually become smaller and smaller until they

cease entirely. When the stimuli recur very frequently, the responses become for a time combined, so that the organ assumes a fixed position unlike the unstimulated one. This quite resembles the condition of a muscle in tetanus, as can be seen by comparing the records in fig. 672. After a period of tetanus, however, the reactions cease until rest from excitation permits recovery. If stimulation, too brief to produce the

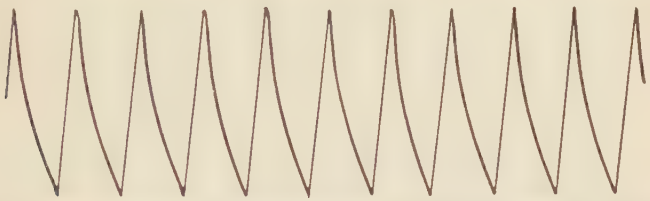


FIG. 671. — Uniform electrical response in radish to repeated stimulation. — After BOSE.

end reaction, be repeated at proper intervals, the separate effects become combined and suffice presently to call forth the end reaction. This *summation of stimulation* seems to be a sort of tetanic piling up of the earlier excitations of the series, which finally becomes sufficient to transmit its effects to the active region.

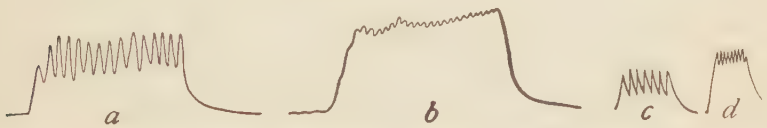


FIG. 672. — Records of tetanic contraction in muscle (*a*, *b*) and in style of *Datura* (*c*, *d*): *a*, *c*, incomplete; *b*, *d*, more complete. — After BOSE.

Reaction time. — Some time elapses between the beginning of stimulation and the end reaction, and this is appropriately called *reaction time*. Whereas in animals this is usually measured by a fraction of a second, in plants it is much longer, occasionally a few seconds, but often minutes or even hours. This tardiness is due not so much to a low degree of sensitiveness, for the first reaction (perception) takes place almost instantly, as to slow propagation and especially to the sluggishness of the mechanism of growth. By contrast, turgor mechanisms usually respond quickly. Naturally the reaction time is made up of the perception time (a small fraction of a second), the transmission time (the rate varies commonly from 0 to 4 cm. per second), and the growth time, which is far the greater part of the whole period.

Presentation time. — In order to produce any reaction a stimulus of given intensity must act for a definite time, called the *presentation time.* For the primary reaction this is extremely brief — practically instantaneous. But end reactions, especially those due to growth, require some minutes or even an hour or more. Thus, roots must be kept horizontal for 15–30 minutes or even longer (depending upon the plant and its condition), in order that gravity may cause a curvature. This means, apparently, that the excitation must reach a given pitch through continuous or summated stimulation, before it can be propagated to the active region and affect the growth mechanism. Once that pitch is attained, the end reaction will follow; and if the initial stimulus cease to act, it will follow as an *after effect.* If the intensity of the stimulus be increased, presentation time is correspondingly shortened (within limits, the ratio is inverse).

Excitability. — To obtain a reaction it is not enough that a stimulus act upon a plant. The protoplasm must be in a certain condition, or excitation cannot follow. This is clearly recognized when it is said that a " dead " plant no longer responds to stimulation as before. It was once said: " The dead organism is ' dead ' merely because it has lost its irritability; " but this is true only by an extension of the term *irritability* beyond its usual sense. Closer study reveals the fact that many agents that do not produce death temporarily abolish or reduce or even exalt excitability. When protoplasm is in a condition of excitability, it is also in a condition to carry on well its usual activities; irritability therefore is associated with other normal physiological qualities covered by the term *tone.* One experiences the feeling of well-being and vigor; it comes when all the functions of the body are proceeding properly. So under favorable conditions the plant's functions are all effective and this *tonic condition* may be assumed as the norm,[1] the result of the combined responses to many simultaneous external and internal stimuli. Retardation or acceleration of particular functions may then be brought about by the intensification or weakening of particular stimuli of this complex, or by the application of unusual ones.

Loss of irritability. — Excitability may be diminished or abolished temporarily by a dose of anesthetics, like chloroform and ether, certain other functions being also interfered with. The precise mode of action is not known. After a time the effect passes away and tonic irritability

[1] Note that this is not a fixed or well-defined condition; it is merely the usual, the ordinary; and it is assumed purely for convenience.

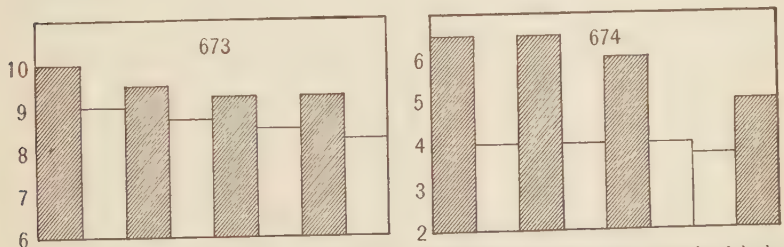
is regained. By a larger dose irritability may be permanently abolished (that is, it kills), while by a smaller dose it may become heightened. Various narcotics act in a similar way. Substances that kill are usually called poisons; really they are poisons only in certain doses. Their modes of action are doubtless as different as the poisons themselves.

In the following sections, the foregoing general principles will find specific illustrations in the movements of locomotion, in the nastic and tropic curvatures of various organs, in the displacement of leaves by motor organs, and in the effects of stimuli upon form. It is important that the principles just set forth be constantly referred to and kept in mind in reading these sections.

3. MORPHOGENIC STIMULI

The most general fashion in which various external agents affect growth appears in the way they control the form of the body through local alterations in the development of various parts. The varied and diffuse stimuli are termed *formative* or *morphogenic*. The reactions to them are extremely difficult to study because both stimuli and reactions are so general, and particularly because experimental alteration of one factor is almost certain to alter others to an unsuspected or an uncontrollable extent; wherefore the analysis of the factors operating is rendered very uncertain. It will be possible, therefore, to mention here only the simpler and best attested examples.

Light and growth. — It is well known that the rate of growth rises and falls with the temperature, and since heat and light are both forms of



FIGS. 673, 674. — Graphs showing growth in millimeters in alternating periods of darkness (shaded) and light: 673, sporangiophore of *Mucor Mucedo*, periods 15 minutes; 674, rhizoids of *Marchantia polymorpha*, periods 20 minutes.—Based on data by STAMEROFF.

radiant energy, it might be expected that the shorter and faster light waves would also affect the rate of growth. This proves to be true. In general the effect of light is to retard growth, particularly in elongating

organs. This is very clearly seen in the sporangiophores of *Mucor* and the rhizoids of *Marchantia*, as will appear from the graphic representation of the observations (figs. 673, 674). It comes out also in the autographic records of the growth of elongating stems when plotted so as to show the increment during the day and during the night, the temperature and other conditions, of course, being kept as constant as practicable.

Daily period. — In nature the retardation due to light is doubtless accentuated by the greater evaporation of the daytime; but it is more

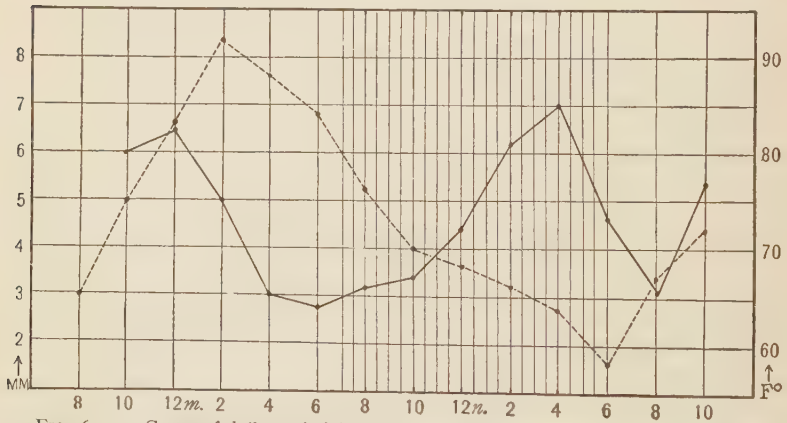


FIG. 675. — Curve of daily period (solid line) and of temperature (broken line): each vertical interval corresponds to 1 mm. increment for the growth curve and to 5° F. for the temperature curve; horizontal intervals are hours, the region of close-set lines showing the night. Note rapid growth during the first day, beginning to fall off before the temperature falls (probably a transpiration effect) and then rising in the night in spite of falling temperature (partly also a moisture effect). — From data by SPOEHR.

or less compensated by the acceleration due to the rising temperature. Contrariwise, the acceleration upon the coming of darkness and a moister air is partly offset by the retardation due to the lower temperature of the night. Nevertheless, a periodic variation in growth in length, corresponding to the day and night, and hence called the *daily period*, can be traced, unless the fluctuations of temperature are excessive. This means that as certain conditions act antagonistically upon the rate of growth, they may be balanced or one set may overcome the other. The difference between the darkness of night and the light of day is so much greater than the usual differences of temperature and moisture in these hours, that the light effect is likely to be dominant (fig. 675).

Light and form. — The form of the aerial parts of most plants is profoundly influenced by light, directly or indirectly. This is shown by the striking changes that ensue (*etiolation*) when they are grown in darkness. Without starvation this is possible only with plants that have already stored a sufficient amount of surplus food. One who has observed the long pallid shoots of a potato which has sprouted in the dark will have seen the general effects. The stems tend to elongate much more than usual, though they are not necessarily more slender; the branching is at a different angle; and the leaves remain small and imperfectly developed. (The pallor from lack of chlorophyll and the presence of carotin are features already mentioned.) On the whole, elongation is likely to be accentuated, breadth is likely to be repressed (fig. 676). Though these are the common results of the lack of light during development, they are by no means universal. Thus, there are plants whose stems do not elongate, and others whose leaves are not reduced. But if not these, other characteristics may be altered; *e.g.* reduction of the mechanical elements of the tissues is one of the less obvious effects. Scarcely a plant escapes but those that pass all their lives in darkness, and only those parts that are buried in the soil are exempt from the formative influence of light.

FIG. 676. — Plant of *Phaseolus* grown in darkness. — After MACDOUGAL.

Dorsiventrality. — In plant organs not grown in darkness, but of which one side is better illuminated than the other, light effects can be observed. One effect is the development of a distinctly different structure in the better lighted surface as compared with the shaded one, and since these are naturally the upper and under surfaces, an organ showing such differences is termed *dorsiventral*.[1] Thus the palisade portion of the mesophyll of leaves owes its existence chiefly to light.[2] Dorsiventrality in the liverworts is likewise due mainly to light. None shows this better than the common *Marchantia*.

[1] Dorsiventral organs may owe the difference of their faces to other formative stimuli, *e.g.* to gravity. See footnote, p. 421.

If a gemma (p. 98), which when separated from the parent is just alike on the two sides, be grown in a moist chamber with the lower side illuminated and the upper dark, air chambers will be developed on the lighted side and rhizoids on the dark one, exactly the reverse of the usual relation. Gravity, if it furnish any stimulus, as is probable, is clearly overcome by light. In like manner light determines the formation of the sex organs upon the under side of fern prothallia. A striking example of light effects among the seed plants is to be found in the dorsiventrality of the rootstocks of the spatter dock (*Nymphaea advena*). These great rhizomes develop at the surface of the mud at the bottom of pools, and are of the length and thickness of a man's arm. From the upper side numerous leaves arise, and from the under side roots. This distribution of organs is found to be determined by differences in lighting.

Electric waves. — Of the same class as heat and light waves are the electric waves; and they too have considerable formative influence. It has been shown that the germination of many seeds is hastened by suitable electric stimuli, and for a considerable time the growth of seedlings is also accelerated. When crops of barley, wheat, beets, and other economic plants are frequently subjected to a quiet discharge of high-tension currents from wires, with many pendent points, strung over the experimental fields, it has been found by several observers that the plants grow better, come to maturity earlier, show increased productivity, and are of better quality than on control plots.

Thus, an electrified wheat plot of 3 acres yielded a crop 39 per cent greater than the control plot, sold at 7.5 per cent higher prices, and the flour was of a higher grade on account of its baking quality. Beets (for the table) on an electrified plot showed 33 per cent increase and contained an average of 8.8 per cent sugar, against 7.7 per cent on the control plot.

Chemical agents. — Chemical stimuli are also extremely important in determining the form of plants. The presence or absence of particular substances in the cells, whether foods or wastes, doubtless exerts a profound influence. But the precise influence of the different compounds cannot be determined satisfactorily, because the chemical processes within the plant are so imperfectly known. It is in this region that the rôle of the so-called necessary elements of the ash, calcium, magnesium, potassium, and iron are to be sought, in all probability. How far the xerophytic structure of plants is to be ascribed to the lack of water is not certain. The deficiency of available water may be in itself a chemical

stimulus, or it may make possible the stimulating action of other substances within the plant, which, but for their increased concentration, would not act so. Unquestionably other causes than lack of water around the roots of a plant may call forth such structures, as is well seen in the case of bog plants. Indeed it has become customary to speak of "physiological" drought as the cause of xerophytic structure, when physical drought is obviously out of the question. This may be taken as a convenient expression for some difficulty which prevents the plant from admitting a sufficient amount of water, such as the poor development of the root system. Whatever does this will tend to dwarf or otherwise transform the aerial parts, either as the plain lack of water does, or possibly in quite different and unrecognized ways. (See further, Part III on dwarfing in bogs.)

Recent investigations are bringing to light some new causes for the imperfect development of plants, which probably is due primarily to an effect on the roots. It is found that the sterility of some soils is due to the presence in these soils of organic substances, which are partly soluble, so that a watery extract of such soils, when used as a water-culture medium, acts as badly as the soil itself. Furthermore, these substances can be removed in large part by adding some finely divided material like lampblack to the liquid and then filtering it out. The filtrate may then be used without detriment to the cultures. Still further study makes it probable that these substances originate in large part from the plants which have previously grown in the soil. The necessity for the rotation of crops on any field has long been known. The reason has been assumed to lie in the exhaustion of the materials which are supposed to be necessary for the nutrition of the plants. Without denying that there may be something in this assumption (it is nothing else at present, because the experimental evidence upon which it rests is faulty), it seems now much more likely that the chief cause is to be found in the excretions from the roots of the previous crops and the products of their decay in the soil. It has been shown that though the mineral salts of a culture solution be maintained unchanged, the water becomes more and more unfit for use with repeated cultures of the same species, and that this impairment may be remedied by treatment with lampblack as above described, though the content of salts be not altered. Water cultures, to which have been added various organic substances that might be produced, or are known to occur in plants, have shown like injuries to the plants, and though the amount of the deleterious substances occurring in nature is too small for direct analysis, their general character may be ascertained by further experimentation in this way.

Mechanical agents. — Pressure and tension have evident influence on the development of mechanical tissues. The encasing of a stem in a plaster cast, so that as it thickens it will compress itself, leads to changes in the structure within the zone of compression and especially just beyond the margin. Continuous tension seems to bring little if any

increase in mechanical tissues, but flexure, with its alternating compression and tension, such as the wind in certain regions produces, beyond doubt increases the proportion of mechanical tissues and thickens their walls. When combined with excessive evaporation and perhaps other unfavorable factors, the effect on bodily form is astonishing (see Part III on stem-dwarfing).

Deformities. — Noteworthy local modifications of form are produced by the attacks of parasites, either plant or animal. When specific deformities are produced, the structures are called *galls* (fig. 655, p. 384). Just how far these are due to chemical substances excreted by the parasite, and how far to the mechanical pressure, to the punctures, or to the movements of the larvae of animal parasites, remains at present quite uncertain. Whether chemical or mechanical stimuli act upon the host, its response might be first an altered metabolism, which produces appropriate effects upon the division and course of development of the cells, resulting in the deformation of the region. Profound alterations in the relative development of the tissues and in the character of their elements accompany the deformity.

Injuries. — Injuries of various sorts call forth growth in tissues which have long passed the ordinary period of cell-division. This gives rise to a callus at the edges of the wound which tends to close it, a fact that is of great practical service in the grafting and budding so indispensable in fruit growing. Desirable sorts, too tender for a given climate, may thus be united with stocks that are hardy, but have no good qualities in their fruit.

In practice, smoothly cut surfaces are opposed and kept in close contact, with the exclusion of water and spores by wrappings and wax. The healing tissues blend, as they form at the junction, and an organic union is established, permitting the passage of water and foods freely.

If a wound be allowed to heal, the callus may give rise to new growing points, from which the regeneration of removed organs may proceed. Thus, if a root be decapitated, a new apex may be regenerated, if the cut be near enough the tip, or new lateral roots may arise that would not otherwise have been produced, or old roots may be incited to more active growth. In either case of the formation of new organs, the reaction to the wound stimulus is complicated with unknown factors named *polarity*, and with the influence of other organs called *correlations*.

Polarity. — Since the opposite ends of an egg cell give rise to unlike structures (for example, in seed plants, suspensor cells from one end and

the embryo initial from the other), it is assumed that the two hemispheres are unlike, even though no structural differences are visible. This is expressed by the term *polarity*, after the analogy of the invisible differences in the two ends or poles of the magnet. A like polarity must be imputed to all other cells, its progeny, so that the embryo initial, when it develops, produces at the one end a root and at the other a shoot. Later in life, any piece of the shoot cut away from the rest shows a tendency to produce shoots at the apical end and roots at the basal end, when put under conditions to regenerate lost organs. The conception of polarity in the cells is thus extended to aggregates of cells of any size, because they show such differences at the apical and basal ends. All attempts to ascertain the nature of polarity have so far proved futile, so that there is nothing to "explain" the phenomena but the word and the assumption for which it stands.

Correlations. — The term *correlation* designates the reciprocal influence of organs. Of this little is known beyond the fact that the suppression or the removal of one organ exercises a marked effect upon some or all of the remaining ones. Many examples might be cited, but no adequate explanation of the effects can be given. It is known, however, that at least some of them are not due merely to differences in the food or water supply, or to like conditions. Examples will make clear what is meant by correlations.

Quantitative correlations. — In the axil of each cotyledon of the bean there is present a bud, neither of which develops into a shoot unless the main axis is cut off or prevented from developing. If one desires sweet peas and such plants to continue flowering, it is necessary to cut away the older flowers or the young pods, so as to prevent the formation of fruit. If this is done, the plants go on flowering till frost, whereas their season is quickly over when allowed to set seed.. The gametophyte of ferns is short-lived, as a rule; but if the fertilization of the egg be prevented, its life may be prolonged for months, and it proliferates, forming archegonia again and again. The possibility of shaping a tree by judicious pruning, and of increasing the production of fruits by orchard trees in the same way, rests upon like reactions.

Qualitative correlations. — Correlations are not merely quantitative, as the above examples might seem to imply; they are also qualitative. That is, the whole behavior and even the structure of an organ may be altered according as other organs are present or absent. Thus, the central axis of most conifers is strictly radial in structure and in branching, while the lateral branches are distinctly dorsiventral. But if the terminal shoot be cut away, one (or more) of the laterals may become erect, losing entirely the dorsiventrality, and becoming radial like the leader. The aerial shoots of the potato, which bear foliage leaves and flowers, are very different from the subterranean ones, which bear the scales and tubers. But if the aerial

shoots be cut away, some of the subterranean shoots will turn up into the air, become green, and develop foliage and flowers as though never inclined to be subterranean. The sporophylls of certain ferns, notably *Onoclea*, are entirely different in aspect from the nutritive leaves, and have so many sporangia crowded on the surface that they seem entirely covered. If all the nutritive leaves be cut away, leaves that ordinarily would have become sporophylls will then become foliage leaves and bear no sporangia. In like manner the tendrils of the pea leaf may be made to develop into leaflets.

In all these cases transformation is possible only before the primordia have gone too far in any determined course, though the point at which new influences may affect them is very different in the different cases. Usually the stimulus must be applied very early, while the primordia are still undifferentiated. Many of the problems of regeneration are complicated by these phenomena of correlation, if they are not wholly determined by them.

4. NASTIC CURVATURES

Epinasty and hyponasty. — A somewhat less general manner in which stimuli of various sorts affect plants is to be found in their effects upon the rate of growth on the two faces of bilateral organs, such as thalli, foliage leaves, bud scales, perianth leaves, etc. It is very common to find that such organs grow at different rates on the two faces, so that they are distinctly curved thereby. Thus, in their earliest stages, the leaves grow fastest on the back or outer side, so that the inner face is pressed close to the axis, and as they usually outgrow it, they curve together over it in a protective fashion, forming a bud. The scales, especially, long maintain this form, as the longitudinal section of any bud will show. Later, the relative rate changes; the inner face grows more rapidly than the outer, and the bud opens because the curvature carries the leaf or scale away from the axis. Thalli often show the same thing; the upper surface may be so tense from greater growth that the thallus is tightly appressed to the ground. Such curvatures are described briefly by the terms *epinasty* or *hyponasty*, according as the greater growth is on the upper (inner) or lower (outer) face. The greater number of these nastic curvatures are due to unknown (internal?) causes, but some have been found to be reactions to external stimuli (paratonic). The former are not unlike those autonomic curvatures of radial organs described as nutations (p. 423), only in this case the bilateral structure of the organ determines that the nutations shall be in one plane only. The latter are also allied to tropisms, but differ from them in that not the direction

from which the stimulus acts but the structure of the organ predetermines the plane of the movement.

Light and temperature. — Examples of paratonic nastic curvature are seen when light and temperature act as stimuli upon foliage and flower leaves, and less plainly in tendrils. Temperature changes are especially effective with the perianth leaves of tulip, crocus, snowdrop, colchicum, and other plants whose blossoms appear very late in the autumn or very early in the spring. In the crocus a rise of half a degree suffices to bring about a curvature that opens the flower; while the tulip can be made to open and close as many as eight times in the course of an hour by raising and lowering the temperature. Tendrils respond to a temperature change, whether a rise or a fall, by curving in one direction only, the upper side being stimulated to accelerated growth. In this they differ from the perianth leaves cited, for in these a rise of temperature tends to accelerate growth on the inner face and thus to open the flower, and a fall to accelerate growth of the outer face and so to close the flower. Very many, perhaps the majority of foliage leaves, show nastic curvatures in response to alterations in temperature and light as long as the petiole is still capable of growing; finally curvature ceases and the fixed light position of maturity is attained. Such bending movements remind one of the photeolic movements executed throughout life by leaves that have motor organs (see p. 451). Among flowers those most strikingly responsive to light are the heads of some Compositae, such as the dandelion. Here the flowers and the bracts about the flower cluster, the involucre, curve so as to close the head when the light is diminished, as in cloudy days, and to open it in sunshine (Part III, figs. 1193, 1194).

In countries where the climate is equable it is possible to select plants whose flowers open at particular hours of the day on account of light and temperature stimuli, and by planting them in a circle to have a sort of floral clock. Naturally it is not very reliable.

Gravity. — Nastic curvatures are also produced in plants in response to gravity, which, however, usually cooperates with or antagonizes the light reactions. In all cases the stimulus at work may be indicated by the prefix. Thus we have photonasty, thermonasty, etc., and still more specifically photepinasty, geohyponasty, etc.

Mechanism. — In all these curvatures the mechanism of response is the same. The growth of the outer or inner surface is accelerated, as can be shown by making equidistant marks upon the two faces and measuring the changes. This observation shows, too, that under frequent

stimulation the total growth is much greater than it is under uniform conditions.

5. LOCOMOTION AND STREAMING

Locomotion limited. — Locomotion is restricted among plants to the simplest forms (with a few exceptions to those that are unicellular), and to the gametes, especially the male gametes, of the multicellular plants. The reason for this is doubtless to be found in the restriction of freedom to move imposed by the cell wall — in effect a sort of strait-jacket — in which the protoplast incases itself. Even when the protoplast moves, as it often does, within this case, its movements do not bear against the outer medium and therefore do not propel it about. The only exception to this restriction occurs in those plants whose wall is perforate; then the protoplasm protrudes through the opening so as to operate against the outer medium, or in a few cases it excretes mucilage forcibly against the medium or the substratum and so pushes itself slowly along.

FIG. 677. — Sperm of *Nephrodium*, with flagella. — After YAMANOUCHI.

Rate. — When the protoplast changes its shape suddenly, quick swimming and darting movements result; when slowly, the movement is perceptible only because magnified by the microscope. In the very swiftest movements the absolute translation is small, say 50 mm. per minute; and in the sperms of ferns, which under the microscope seem to be going fast, the rate is only 0.1 to 0.2 mm. per minute. Measured relatively, as in terms of size, and taking account of the resistance of the medium, the translation is seen to be very rapid. The very fast human runners cover about 50 times their own length (100 yards) in 10 seconds; the swarm spores of *Ulva* can travel 100 times their own length in the same time; and the spiral sperms of a fern (*Nephrodium*) can do 50 to 100 times their length (as coiled) in 10 seconds (fig. 677).

Amoeboid movements. — The slow movements are a kind of creeping, and are of two sorts, amoeboid and excretory. Amoeboid movements (so called because characteristic of *Amoeba*, a genus of infusoria) are found rarely among plants, being known only in the plasmodia of Myxomycetes, a group of organisms with so many animal characters that they

are often included in the animal kingdom (see p. 1). The plasmodium is a naked mass of protoplasm (sometimes like a thin cake, often a richly anastomosed network), which during its vegetative period lives in wet places among decaying wood, leaves, etc. The creeping is accomplished by the protrusion of marginal lobes of the protoplast along one side, and toward these the rest slowly flows. In this way the whole mass advances in a definite direction, which is frequently changed and is subject to control by external agents. Thus, by varying the temperature, the moisture, or the illumination, the plasmodium may be made to creep in one direction or another. Its response to these stimuli, however, differs with its own stage of development. Whereas during a considerable vegetative period it avoids light and drier places, later it creeps out from the substratum and ascends to drier and exposed situations, where it produces sporangia with a casing and framework of cellulose and a multitude of spores.

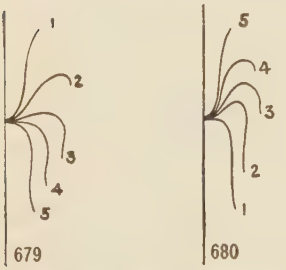
Excretory movements. — Excretory movements are executed by some diatoms and desmids, and those of *Oscillatoria* and *Spirogyra* are probably of this sort. The diatoms and desmids forcibly excrete mucilage through slits or pores in the wall against the substratum (a glass slide, the wall of an aquarium, the bottom of a pool, or the surface of a water plant) over which they creep slowly with a majestic and mysterious motion, which is not yet fully understood (see also p. 451).

Ciliary movement. — The more rapid movements are called ciliary, because executed by the lashing of slender threads of protoplasm through the water, in which alone such organisms can move. The motile threads are known as *cilia* or *flagella*.[1] They arise from different places on the protoplast, often at the pointed apex or along a band, where the special organ which produces them, the blepharoplast, is located (fig. 678). The flagellates (unicellular organisms of uncertain relationship, p. 20), bacteria, the zoospores and gametes of certain algae and fungi, and the sperms of bryophytes, pteridophytes, and

FIG. 678. Swarm spore of *Hydrodictyon*, with two cilia arising from a blepharoplast with nuclear connections. — After TIMBERLAKE.

[1] No constant distinction can be made between cilia, which are typically short, hairlike, and numerous, and flagella, which are long, whiplike, and few (1–4) for each cell. Yet a cell sometimes has a single cilium, or two, and flagella are numerous on the sperms of ferns.

cycads, exhibit ciliary locomotion. The cilia are so slender, and when magnified sufficiently their movements are so rapid, that the details of the strokes are difficult to follow. In the thicker cilia of infusoria the forward stroke (fig. 679) consists of a progressive bending, which begins below the free tip and advances to the base, where it is most powerful. At the moment of greatest efficiency (fig. 679, 2), the curve bears against the water like the blade of an exaggerated spoon oar (though, of course, the cilium is not flattened). The return stroke (fig. 680) is slower and consists of a reverse and somewhat different curvature, advancing from base to apex.



FIGS. 679, 680. — Diagrammatic representation of sucessive positions (as numbered) of cilia of *Urostyla grandis;* 679, in forward stroke; 680, in recovery. — After VERWORN.

Cause. — The cause of these repeated lashings is completely hidden. They continue for a time and then cease. Though they cannot be initiated, they can be stopped or modified in rate by appropriate stimuli, and their duration can be prolonged. Thus, if zoospores of algae be released in light, they may swim about for a few hours, then attach themselves and germinate. But if they be kept in darkness, the swimming may continue for two or three days, until the zoospore seems entirely exhausted and perishes without settling down.

Taxies. — The direction of swimming may also be controlled by external agents. The phenomena of directed locomotion are comprehensively called taxies, and with a prefix, designating the directive agent, we have phototaxy, thermotaxy, chemotaxy, etc. These responses, apparently simple, are really very difficult to interpret, and experiments, seemingly quite conclusive, may lead to false inferences through the operation of some overlooked factor. Thus, if a dish containing zoospores of algae be placed on a window ledge so that one side is more brightly illuminated than the other, the swarm spores will be seen to accumulate on the side with brighter light, and this movement was described at first as a positive response to light. Later it was found that the droplets in an oil emulsion would behave in the same way because of the previously unnoticed differences in temperature, making convection currents in the dish. Two factors were therefore involved and more rigid tests were needed to demonstrate phototaxy.

Chemotaxy. — Chemotaxy has been most extensively investigated, but is not yet fully elucidated. If a soluble crystal be introduced into water undisturbed by currents, the molecules gradually diffuse from its surface in a constantly enlarging sphere; or if the water be the film under a cover glass, in an increasing zone. By using a glass tube drawn out to a very fine capillary and closed at one end, liquids of any sort may be used. A short capillary is filled with the solution and placed on a microscope slide with its open end under the cover glass. Slow diffusion takes place from the mouth, while the behavior of the organisms is watched under the microscope. As a rule the rate of their movement is not affected, except by substances that are directly injurious. It appears that the directive effect of such stimuli is exercised in two different ways.

1. **Orienting reaction.** — In the first case, the direction is altered because the organism, in response to the stimulation, orients itself, so that with continued movement the body will be carried toward or away from the source of the diffusing molecules. It is assumed that this orientation is determined by the unequal or one-sided action of the molecules, the end (less probably the flank) toward the source being most powerfully affected, whereupon the creature turns, and according as it brings the anterior or the posterior end toward the source of stimulus, and swims, it will approach or recede from that source.

2. **Recoil reaction.** — The second case is quite different. The movements of sperms and zoospores are too rapid to be followed easily; but if large and slow-moving organisms are observed, they may be seen to swim about quite indifferently, passing in close proximity to the crystal or capillary tube from which the molecules are diffusing, without showing any tendency to swim towards it. But when they reach by chance the limits of the diffusion zone, they suddenly reverse their direction and back away, as though they had encountered an obstacle and had rebounded from it. This reaction is repeated at every side, and having once chanced to swim into the diffusion zone, they are imprisoned within it, because the attempt to pass out of it results always in the reaction of recoil. So, as more and more are thus caught, there is an accumulation within the diffusion zone, as though it were a trap. Not all substances, however, permit the first accidental entry, for the recoil may be produced at the attempt to enter this zone, while any such organisms placed within it would be free to swim out without recoil. In such a case the final result is the accumulation of the organisms in the regions

outside the diffusion zone. Besides the reaction of recoil, there are accompanying minor reactions which cannot be discussed here.

Attraction and repulsion. — Many different substances have been tested with respect to chemotactic control. Some prove to be attractive, some indifferent, and some repellent. That responses occur to substances that are never met in nature, as well as to those that are not foods, and further, that they do not prevent the organisms from coming to serious or even fatal injury, indicates that chemotaxy depends upon some fundamental property of the protoplasm and is not a mere adaptation to secure special ends, however well it may occasionally serve such a purpose. In many cases a substance which is attractive at a low concentration proves to be repellent at a higher. In such a case the question arises whether the repellent action is due to the chemical constitution of the stimulant or to the osmotic pressure of its solution. As the latter seems to be the reason for the action in certain cases, the phenomenon is named *osmotaxy*. It has not yet been sufficiently investigated, but is in many ways parallel to chemotactic irritability.

Amount effective. — The amount of a substance which can act directively upon motile organisms is infinitesimal. Thus it was found that a minute capillary into which the sperms of a fern crowded, contained, all told, less than three hundred-millionths of a milligram (0.000000028 mg.) of malic acid. Of this, certainly, only a very small fraction could have reached any one of the sperms. Yet relatively the amount is not at all insignificant; for the estimated weight of one of the sperms is only ten times greater than the total weight of the acid, and if only 1/100,000 of the total acted upon a sperm, the ratio would be 1 : 1,000,000, which is still 10 times the ratio of a minimum effective dose of morphin for the human body.

Weber's law. — The phenomena of chemotaxy offer an excellent illustration of a general law of response known as *Weber's law*. If a fern sperm is swimming in water, it will be diverted toward a capillary containing malic acid whose concentration is 1 part in 100,000 of water. But if it is brought into a solution too weak to evoke a response, say 1 : 200,000, it is so affected by the enveloping acid that it does not respond unless the solution in the capillary is 30 times as strong as that by which it is surrounded, *i.e.* 30 : 200,000. If again the concentration of the acid in the medium be raised, say from 1 : 200,000 to 1 : 100,000, the concentration of the stimulant in the tube must be 30 times greater, *i.e.*, 30 : 100,000, in order to evoke response; and so on. It

appears from this that a sensitive organism becomes adjusted to a constant non-directive stimulus, and then is unresponsive to an intensity of one-sided stimulus of the same sort, to which in the unaccustomed state it reacts. Thus accommodation is really a lowering of irritability toward a particular stimulus. The noteworthy point is that it is a proportional lowering; for, after each adjustment has occurred, it requires a definite increase in intensity (in this particular case a large one — 30 times the constant) to call forth a response. Some ratio of this kind, whether it be an increase of 3 times or 30 times the constantly acting stimulus, has been found to hold good for many forms of response and in many sorts of organisms. In all cases the law is valid for moderate stimuli only; an intensity is soon reached where it ceases to express the facts.

The law was formulated in 1834, with reference to touch and sight. It has been stated lately thus: "The smallest change in the magnitude of a stimulus which will call forth a response always bears the same proportion to the whole stimulus."

Aerotaxy. — One form of chemotaxy has received a special name, *aerotaxy*, which signifies that the air, or more exactly the oxygen of the air, is the excitant. Certain forms of bacteria are motile only when they are in contact with oxygen, and cease to move when they are deprived of it. In so far, this also might be due merely to respiratory disturbance, just as many functions cease when no oxygen is supplied. But these forms also swim in the direction from which the oxygen is diffusing, and accumulate about its source. Such forms, if evenly distributed under a cover-glass, soon desert the center and gradually accumulate at the edge, where the O_2 is diffusing into the water. These species, motile in oxygen, can be used as indicators of photosynthesis, because O_2 is a by-product.

Ionic stimuli. — All chemotactic reactions to substances that dissociate in water probably rest upon the specific action of the various ions and molecules present in the solution, and attempts have been made to correlate the action of the various salts and acids. But the phenomena are too complex to permit satisfactory analysis yet; and since undissociable substances also act as stimuli, it is probable that the undissociated molecules, as well as the ions, have a stimulating action in many cases.

Phototaxy. — Phototaxy is particularly characteristic of those organisms that have chlorophyll, such as the zoospores of algae and the ciliated colonial algae like *Volvox*, *Eudorina*, etc.[1] That they swim towards light of moderate intensity is not to be doubted; but it has been very

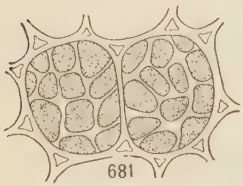
[1] Some fungus swarm spores also are sensitive to light.

difficult to determine whether this response is due to the direction of the light rays, or to the fact that one region is more brightly illuminated than another. Accumulation certainly occurs in regions of moderate light, with avoidance of the more shaded or the more brightly illuminated portions. The most exact of the recent studies of *Volvox* shows that its orientation is controlled by the relative intensity of the illumination on different sides of the colony, and as it swims with a definite pole forward, swimming after orientation causes it to move nearly parallel with the rays, some deflections from this course being due to certain minor disturbing factors.

In phototaxy, as in chemotaxy, organisms respond both by orientation and by recoil, though, so far as known, the latter is much less common. The light waves vary in action according to their length, the reds and yellows, though the brightest, being quite unstimulating, whereas the blues are most effective. Yet this gives no clew to the real nature of the excitation or of the organs by which it is perceived.

Geotaxy. — Certain organisms have also been found to be geotactic. This property is quite distinct from others; for organisms that respond alike to other stimuli, such as light and oxygen, may react differently to gravity, the one being positively, the other negatively geotactic. Upon such irritability may depend the ability of the creatures to rise or sink through the water on occasion.

Motion of cell organs. — Not unrelated to the movements of free-swimming organisms that have been described are the movements of organs of the cell which take place within the limits set by the wall. Such, particularly, are the movements of the chloroplasts and the nucleus. The former are known to be in part responses to light stimuli. Certain algae of the genus *Mougeotia* (*Mesocarpus*) have a single platelike chloroplast, which lies in the axis of the cell, facing the incident light, when this is of appropriate intensity. But if the light becomes more intense, the plate rotates until the edge is presented to the light. The numerous rounded chloroplasts of seed plants, mosses, etc., alter their distribution and their shape according to the illumination (figs. 681, 682, and in Part III, figs. 758, 759). This suggests a sort of escape from too bright light,



FIGS. 681, 682. — Two leaf cells of a moss (*Atrichum undulatum*) seen from above: the chloroplasts in 681 in epistrophe; in 682, in apostrophe. — After SCHIMPER.

an idea that agrees with what is known of the intensity of light required for photosynthesis (see p. 371). Yet the arrangement is seldom as regular or complete as it is sometimes described, and effective protection from light is secured mainly in other ways. Aside from their own amoeboid movements the chloroplasts are subject to displacement by movements of the protoplast, as in streaming (below).

The nucleus also changes its position in the cell "spontaneously" or in response to certain stimuli, notably to wounding. Nothing is known as to the significance or mechanism of such movements.

Streaming. — In very many active cells a streaming movement of portions of the protoplasm has been observed. The layer closest to the wall does not participate in the movement, and though the chloroplasts, when any are present, are not necessarily involved, they are often swept along when they lie deeper. The rate of the motion varies with temperature and with other conditions that affect the general activity of the protoplasm, and the movement may be entirely stopped by appropriate stimuli. Nothing is known as to the causes or the effects of these movements, though they are extremely common and perhaps universal. The idea that they facilitate the more rapid distribution of foods and solutes in the cells and so hasten osmotic transfer of materials would be more plausible were streaming less common and vigorous in those cells, *e.g.* in hairs, where such a process seems of slight importance.

In some diatoms the protoplasm partly protrudes through a longitudinal median slit (the raphe) in the valves, and streaming movements in this outer belt, reacting against the water or the substratum, propel the cell slowly in the direction opposite to the outer streaming. The counter-stream, of course, moves within the cell wall.

Surging movements of the protoplasm in the coenocytic hyphae of *Mucor* and other fungi have been seen, but their causation and significance are unknown.

6. TURGOR MOVEMENTS

Motor organs. — In a considerable number of plants thin-walled turgid cells are so arranged that the position of the organ of which they form a part depends upon the relative turgor of these cells. In most cases the organs are leaves, either foliage or flower leaves, and the structure is such that the *motor organ* curves only in one plane, the distal part rising or falling with the variations of turgor. Examples of these motor organs are afforded by the leaves and leaflets of the Leguminosae and the Oxalidaceae, by the stamens of *Berberis*, and by the stigmas of *Mimulus*;

they are also found in a considerable number of families allied to the Berberidaceae and Scrophulariaceae.

Structure. — The leaves of Leguminosae are usually much branched, and the primary motor organ, when present, is located at the base of the main petiole. In many cases there are also motor organs (secondary) at the origin of the secondary petioles, and if the leaf is ternately compound the petiolules or stalks of the leaflets are motor organs. Thus *Mimosa* has primary, secondary, and tertiary motor organs (fig. 683); but the red and sweet clovers have only one set, the stalks of the leaflets. The motor organ consists of all or a portion of the petiole or petiolule, modified by changes in the position of the vascular bundles, and by an excessive development of the parenchyma of the cortex. Through the greater part of the leaf stalk the vascular bundles lie at some distance from the center, surrounding a distinct pith, and within a cortex of moderate thickness. In the motor organ, however, they approach one another so closely that there is scarcely any central pith, and they form a shaft, elliptical or kidney-shaped in section. Outside, the cortex is correspondingly larger, and its cells are usually somewhat different from the rest. As a whole the motor organ is sometimes thicker than the other part of the petiole, but it is quite as likely to be smaller; in all cases, however, the relative increase of the cortex in cross section gives the impression of a cushion of parenchyma.[1] In this region the cells are rather regular in form, approximately cylindric, and with smaller intercellular spaces than in the nutritive regions. Intercellular spaces are present, however, at the junction of three or more cells.

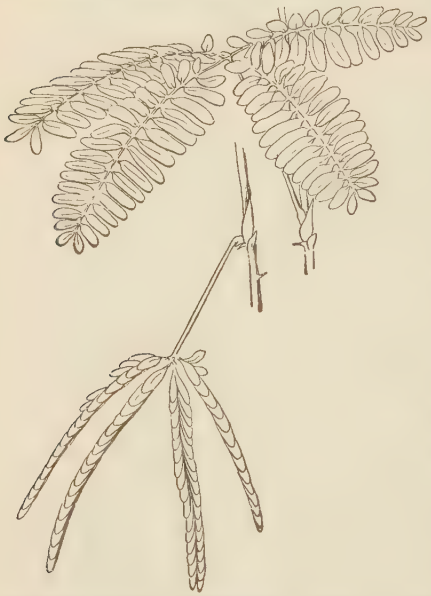


FIG. 683. — Leaf of *Mimosa* in open and closed positions. — From PART III.

[1] This is the reason for a technical name applied to the motor organ, the *pulvinus*.

Mechanism. — It is evident that the central position of the vascular bundles permits flexure more readily than if they were scattered and more peripheral; while the peripheral position of the thin-walled cells of the cortex is such that any variation in their turgor will produce a curvature, the side with less turgor becoming concave, since its cells no longer oppose fully the turgid cells of the opposite side. Correspondingly, the parts beyond the curving motor organ will be displaced by it. These turgor variations, due to modified permeability, being usually restricted to the upper and lower sides of the motor organ, the distal parts are moved up and down. Since the relaxed cells may recover turgidity and the turgid cells become flaccid, the notable feature of all such movements is that the changes in the cells are *reversible;* whereas the cell changes involved in growth are *irreversible* (or soon become so).

The motor organs of stigmas and stamens are essentially similar to those of foliage leaves, but simpler, since vascular tissues are slightly or not at all developed, and almost the whole tissue is parenchymatous.

Autonomic movements. — The variations in turgor are sometimes autonomic, that is, determined by causes unknown and apparently internal to the plant, but more commonly they are controlled by external stimuli. Autonomic movements are not at all uncommon, but they are mostly too slow to be observed easily without apparatus, and, when sought, are often masked by more obvious movements (see p. 457). The classical and almost the only striking example of easily seen movements is offered by *Desmodium gyrans,* whose lateral leaflets (fig. 684) are constantly rising and falling under favorable conditions. These movements, sometimes uniform, but usually jerky, are not very rapid, for a complete up-and-down movement requires 2–4 minutes. The fall is more rapid than the rise (for example, 45 sec. as against 70); and as the turgor variations tend to fluctuate regularly to right and left of the vertical plane, the tip of each leaflet describes a narrow ellipse. The reason for these movements is unknown, nor are they known to be of any value to the plant.

FIG. 684. — Leaf of telegraph plant (*Desmodium gyrans*), natural size: *l*, *l*, lateral leaflets which show autonomous movements; the terminal leaflet in the depressed position. — After PFEFFER.

Under unfavorable conditions they cease, but the plant may still be able to respond to external stimuli like others about to be described.

Paratonic movements. — The terminal leaflet of *Desmodium gyrans*, like leaves of other members of the bean family, exhibits *paratonic* movements (*i.e.* those due to special stimuli, not tonic; opposed to autonomic). Moreover, some plants whose leaflets ordinarily exhibit only paratonic movements, may make autonomic ones under exceptionally favorable conditions. Thus it would seem that there is no fundamental difference in the two, and when the precise stimuli that initiate the movement are discovered, autonomic movements may all be relegated to the paratonic category.

Turgor movements due to external stimuli are numerous and easily observed, but except in a few striking cases they are not rapid enough to be seen by watching for a brief time. The stimuli initiating the movements are of the most varied character; contact, gravity, and changes of light and temperature being the most common.

Contact movements. — If the stamens of the barberry (*Berberis*) be touched near the base at the time when they are shedding pollen, they suddenly fly up and inward, carrying the anthers close to the stigma. After a short time they resume their former position against the petals. The filaments of the Cynareae, a tribe of Compositae, shorten instantly on being touched (the reaction time is less than 1 sec.), dragging the coherent anthers quickly down over the style, whose hairs scrape out the pollen like a pipe cleaner. In *Centaurea americana*, this contraction continues for 7–13 seconds, and after a minute the rest position is again reached.

FIG. 685. — Leaf of sundew (*Drosera rotundifolia*) with half of the tentacles inflexed from stimulation. — Adapted from KERNER.

Probably the best known of the rapid contact movements are those of the species of *Mimosa* and *Biophytum*, the "sensitive plants." In *Mimosa* the leaflets are carried by the motor organs forward and upward until the upper faces are pressed together, while the primary motor organ drops the whole leaf (fig. 683, p. 452). Another famous example is the quick closure of the "fly-trap" of *Dionaea* (figs. 657, 658, p. 386). Here

the motor organ lies along the central rib, between the two lobes of the leaf, and when an insect touches one of the three sensitive bristles on either face, these lobes shut together quickly like the jaws of a trap, and their interlocking teeth prevent the prey from crawling out easily. After a time the superficial glands pour out a secretion containing an enzyme that digests the proteins, and these are absorbed and utilized as food. After several days the trap again opens. Somewhat slower movements are made by the "tentacles" of *Drosera* (fig. 685). When an insect is entangled in the viscid secretion at the tips of these leaf lobes, its struggles furnish a stimulus which results in the incurving of all, until it is completely enveloped in their secretion, which then changes character, becoming digestive, and so prepares the proteins for absorption (see p. 388).

Gravity movements. — Gravity cannot act as a stimulus unless the plant be displaced. If a potted bean plant be turned upside down or laid on the side, in a few hours the motor organs become curved so as to bring the leaves again into the usual position, or as near to it as possible.

Photeolic movements. — The most striking movements are the regular ones produced by motor organs under periodic stimulation by variations in the intensity of light (and temperature). These have been known under the misleading name of "sleep movements," because they are notable at nightfall. However, they have no similarity whatever to the relaxed position assumed by animals in sleep, nor do they bring any recovery from fatigue. On the contrary, the nocturnal position is one of precisely as much strain as the diurnal one, since the resistance of the motor organ to bending is measurably the same; and even the position is as likely to be erect as drooping.

Technically they have been called *nyctitropic* movements, but as the curvature is not a tropic one this term is objectionable, and the more so as the movements are quite as much associated with day as with night. They are best called photeolic (*i.e.* light variation) movements, because the illumination is chiefly responsible for them, though corresponding fluctuations in temperature accompany the changes in light and sometimes cooperate in setting up the movement.

Photeolic movements consist of a rising or falling, a forward or backward movement, of the entire leaf and (if the leaf be compound) of all the leaflets as well; or the leaflets alone of a compound leaf may exhibit such movements. The change in the leaves of the common purslane (figs. 686, 687) will make clear the general character of these changes

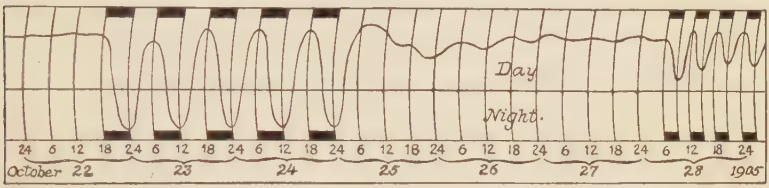
of position, which are executed by differences of turgor on opposite sides of motor organs appropriately situated. Inasmuch as the changes in illumination are not sudden (in nature), it should be expected that the movements would not be restricted to morning and nightfall. In fact it can be shown that there is really a slow variation, so that in the brightest hours of the day the blades reach their highest or lowest position, the opposite being attained in the maximum darkness. As the changes in the intensity of the light are most marked at dawn and at dusk, the changes of position are then most rapid and so attract attention.

FIGS. 686, 687. — Shoot of the purslane (*Portulaca oleracea*), photographed from identical position at 2 P.M. (686) and at 8.30 P.M. (687); note that the older leaves show little change of position. — From photograph by LAND.

Persistence. — To these periodic variations in light the plant becomes habituated, and even if they are not allowed to occur, as when a plant is kept in continuous darkness or continuous light, the movements continue, with diminishing amplitude, for a considerable time (3–5 days) before they cease entirely. The normal periodic stimulation seems to have impressed upon the protoplast a rhythmic variation in turgor, so that it cannot at once cease the customary action even when no stimulus demands a reaction (fig. 688).

When these movements are ceasing, there come to view similar ones which are usually masked by the photeolic reactions. These, however, are autonomous; they are much less extensive and have a much shorter period than the others. When sought, they can be observed even in the presence of the photeolic movements. They consist of a pendulum-like swinging of the leaf or leaflets, up and down (somewhat as in *Desmodium*, fig. 684; see also fig. 689), whose advantage and effects are alike obscure.

Advantage. — The benefits of photeolic movements have been variously imagined. They have been supposed to prevent injury to the leaves by frost, since the folded position diminishes radiation; or to prevent the formation of dew, so that transpiration may begin promptly in the morning. The difficulty with the first of these ideas is that frost does not occur in the regions where Leguminosae, which exhibit them more strikingly than any other family, most abound; furthermore, a temperature approaching 0° C. would render response impossible. The second explanation involves the assumption that transpiration is a valu-



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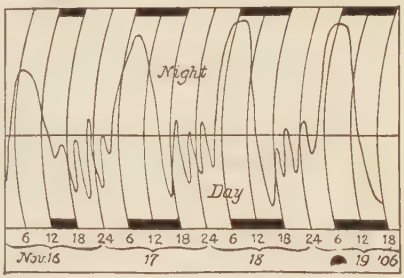


FIGS. 688, 689. — Autographic records of leaf movements: dates and hours of the day are given below; 12 noon, 24 midnight; the horizontal median line represents the line the recording point would have described had the leaf remained quiet, moving neither toward the diurnal (*day*) nor the nocturnal (*night*) positions; the black strips mark the periods of darkening, which have no relation to the natural alternation of day and night; 688, photeolic movements of leaf of *Albizzia lophantha;* after a period of constant illumination the plant was subjected to 6-hr. periods of alternating darkness and light, then to continuous light, and finally to 3-hr. periods of alternate darkness and light; note the persistence in light (Oct. 25–27) of the movements, which gradually disappear; 689, photeolic and autonomous movements of leaf of *Phaseolus vitellinus*, the latter restricted to the reversed periods of illumination (6 P.M. to 6 A.M.); note the lag of the response in the former. — After PFEFFER.

able function which the plant promotes, instead of a danger that menaces its very life. It is difficult to conceive the significance of these movements in terms of welfare, and it is quite possible that they have none.

Other stimuli. — Changes in temperature, which often coincide and cooperate with changes of light in producing photeolic movements, may act alone, and, when sufficient, call forth like responses. Severe injury, even when wrought without mechanical disturbance, as by burning with a lens, will also stimulate the motor organs to curvature. So will a variety of other stimuli.

Growth movements and turgor movements. — The intimate relations that exist between turgor and growth, as well as the suddenness of their response under favorable conditions, make it possible that the first curvature of tendrils (see p. 471) is due to quick alterations in the turgor of the cortical parenchyma. If this be true, the turgor curvature is followed promptly by unequal growth, to which irreversible process the more permanent and more important of the tendril movements are due. Their behavior will therefore be discussed in connection with growth movements. Indeed it is not improbable that turgor changes underlie all such movements, though they are not apparent.

In many plants whose leaves have no well-defined motor organs there exist slight modifications of structure looking in the same direction, with movements of less extent than those executed by well-developed motor organs. Moreover, there are to be found similar movements in young leaves that have no trace of motor organs, but these movements cease by the time the leaves have attained mature size. (Compare young and old leaves in figs. 686, 687.) Doubtless growth, that is, irreversible changes in the size of the cells, as contrasted with the reversible changes produced by turgor, cause these movements.

From the foregoing it is evident that no hard and fast line can be drawn between the displacements due to turgor and those due to growth. In fact there are all gradations between them. Therefore, the separate treatment must not be permitted to establish in the mind too sharp distinctions; for distinctions are valuable chiefly as conveniences to the memory; they have usually slight basis in nature.

7. TROPISMS

Growth curvatures. — It is a matter of common observation that the various parts of a plant have definite positions. If they are mechanically displaced, the usual position often is resumed after a time by curvature. Again, if some external force acts upon them from an unaccustomed direction, a curvature may result, restoring the customary relations so far as may be. Some of these curvatures have been considered; namely, those that are due to changes of turgor. But a much larger number are due to growth, because few plants have such a structure as to permit turgor variations to move an organ. On the contrary, every plant has some part where growth is either in progress or can be initiated, and consequently a curvature can be induced, if by appropriate mechanisms the amount or rate of growth can be modified locally. Practically all plants have such mechanisms, which are set into operation by various external stimuli. It will be most convenient to consider these *tropic* curvatures according to the stimulus that induces the reaction.

Parallelotropic and plagiotropic organs. — Observation shows that in certain plants the main axes respond to a tropic stimulus by placing themselves parallel to the direction from which the stimulus acts, while other

parts, such as the branches or leaves, set themselves at a definite angle to the line of the stimulus. Other plants may place even the main axes at an angle to the stimulus. This difference of behavior is expressed by the terms *parallelotropic* and *plagiotropic*, applied to the organ concerned.

Because responses to tropic stimuli lead so often to the erect position of axes, such axes were first called *orthotropic* organs, and their correlates were called plagiotropic, with reference merely to position. No confusion can arise from the substitution of the more specific term *parallelotropic*, and the use of plagiotropic in a somewhat modified sense.

(1) Geotropism

The stimulus. — No force acts so constantly and so equally in all parts of the earth and in all situations as gravity. It might be expected, therefore, that it would have some influence upon the position that the parts of plants assume. If there were nothing more to be observed than that the main stems of so many plants in all countries are directed away from the center of the earth, this would suggest the agency of some general stimulus. But it is easy to observe that as soon as a plant stem which usually grows erect is overthrown, curvatures occur in the younger parts that again direct the apex upward, though the older parts are unable to erect themselves. Fallen trees, and corn or other cereals beaten down by wind and rain, offer many examples, and the simplest experiments suffice to demonstrate the main facts; namely, that gravity is the stimulus, and unequal growth the end reaction.

The first demonstrative experiments were conducted at the beginning of the last century, by affixing boxes to the rim of a wheel, which could be rotated either in the vertical or the horizontal plane, and planting seeds in these boxes. When the seedlings appeared on the vertically placed wheel, they seemed to have quite lost their way, growing in any direction in which they happened to be pointed when they broke through the soil; and some did not even emerge. On the horizontal wheel, however, no difference was apparent when it was rotated slowly; but when it was turned rapidly enough to introduce a considerable centrifugal acceleration ("centrifugal force"), the usual position of the axes was changed, the stems which would normally grow erect tending to direct themselves toward the center of the wheel, and the primary roots, which usually grow downwards, growing toward the periphery; and these tendencies were the more pronounced the more rapid the rotation.

This mode of experimentation is universally used when one wishes to equalize or modify the action of any one-sided stimulus. In all such experiments it is essen-

tial to arrange the plants so that the only factor in their environment that is altered is the direction from which the stimulus acts. The clumsy wheel has been replaced by the modern *clinostat*, a disk to which potted plants can be conveniently attached and capable of rotation in any plane, continuously or intermittently, at a very even speed [1] by strong clockwork or by a water or electric motor. The centrifuge is a modification whose disk is driven at a high speed when centrifugal acceleration is to be compared with gravitational.

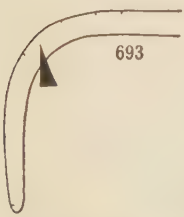
Parallelotropic organs. — The behavior of parallelotropic and plagiotropic organs differs in certain particulars. The former will first be considered. Parallelotropic stems in responding to gravity curve so as to erect their apices when displaced. Primary roots, which are usually directed straight downwards, when displaced respond by turning the tip toward the earth. These responses, in quite opposite directions, arise from an identical original stimulus. By some mechanism within the plant body the end reaction is made different. It is convenient to distinguish the difference by assuming some difference in the sensitiveness. So the special term *positive geotropism* or *progeotropism* is used to designate the property by which the growing point is directed toward the center of the earth, and *negative geotropism* or *apogeotropism* that by which the tip is turned away from it. The curvature might be due (*a*) to unequal retardation of growth along both sides; or (*b*) to unequal acceleration of growth along both sides; or (*c*) to an unchanged rate of growth on one side with either acceleration or retardation on the other; or finally (*d*) to simultaneous retardation on one side and acceleration on the other. It has been determined that usually, in both stems and roots, gravity accelerates growth, but the segments are unequally affected according to position (case *b*). In the one case (apogeotropism), the lower side is caused to grow more rapidly than the upper; in the other (progeotropism), the upper side grows more rapidly than the lower. How this difference in action is brought about is quite unknown.

Course of curvature. — The course of curvature in a parallelotropic stem continuously stimulated by being laid horizontal shows an interesting example of "after-effects." The reaction time is usually some hours in length. When the apex has reached the erect posture again, it might be supposed that it would go no further. On the contrary, it is carried past the vertical, responding to the excitation set up some hours before. Being thus carried beyond the position of equilibrium, it is stimulated

[1] Otherwise any exact experiments may be vitiated by errors due to unequal stimulation, a common fault with makeshift clock clinostats, which suffice, however, for elementary demonstrations.

to a reverse curvature, and this also, by reason of continued stimulation during the long reaction time, may again carry the tip past the vertical; thus, only by a series of pendulum-like swings is the position of equilibrium attained. The successive positions of the stem of *Impatiens* shows the way in which such a stem erects itself (fig. 690). It shows also that the curvature begins in the region of most active growth and gradually affects less active regions, becoming permanent finally as the tissues of the growing region most remote from the apex cease to grow.

FIG. 690. — Successive positions, from photographs, of *Impatiens glanduligera* in erecting itself from the horizontal. — After PFEFFER.



FIGS. 691–693. — Geotropic curvature of a root of *Vicia Faba*: 691, placed horizontal; 692, seven hours later; 693, twenty-three hours later. — After SACHS.

That the curvature appears in the region of most active elongation is clearly shown by the behavior of certain roots. If a suitable one be marked at intervals of 1 mm. and then fixed in a horizontal position, it will be found after some hours that curvature is taking place in the third and fourth of these divisions; after twenty-four hours it is easy to see that the second and third divisions have grown most, though the chief curvature still persists in the fourth division that was growing most rapidly (figs. 691–693).

Presentation time. — It is not necessary to continue stimulation until the reaction appears. In other words reaction time is longer than presentation time. These periods are, of course, very variable. The shortest presentation time recorded for geotropic curvature is 2–3 minutes (cut shoots of *Capsella*, hypocotyls of *Helianthus*, and peduncles of *Plantago*). In many plants it is 15–25 minutes; in less sensitive plants it is double or treble this, or even extends to several hours. Both periods are greatly influenced by temperature. Thus, a seedling of *Vicia Faba*, having at 14° C. a presentation time of 70 minutes and a reaction time of 120 minutes, had these periods at 30° C. respectively

10 minutes and 48 minutes. The longer the stimulation, other things being equal, the more marked the curvature; from which it is evident that there is an increase of the excitation with continued stimulation, and thereby the end reaction becomes more marked.

Summation. — Contrariwise, it should be expected that stimulation too short to result in curvature would not be without effect. That it does produce excitation is shown by the fact that if a plant be placed alternately horizontal and erect, each period of stimulation being shorter than the presentation time for that particular plant, and the interval of rest shorter than is needed for recovery, curvature will finally occur. Evidently this is a cumulative effect; yet it is not a summation of the total successive excitations that occur during the times of horizontality, but only of the residual excitation. For, if a suitable plant be placed horizontal for 30 minutes continuously, the reaction curvature is more pronounced than if it be so placed for ten 3-minute periods at 10-minute intervals. Clearly, while erect, the preceding excitation is slowly disappearing, and if the interval before the next stimulation is too long, recovery will be complete and no evidence of the excitation will appear in the form of curvature.[1] In such experiments, therefore, it is necessary to apportion properly the intervals of rest and stimulation.

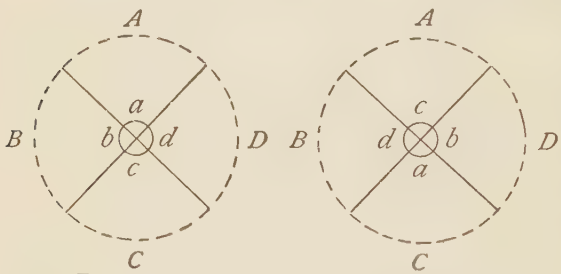


FIG. 694. — Diagram: for explanation, see text.

Rotation. — From the above considerations it will be evident that when a plant is rotated in the horizontal plane on a clinostat, its failure to execute any curvature is not at all due to a lack of excitation, for while the side *a* of the stem is passing through quadrant *A* of its rotation (fig. 694), quadrants *a* and *c* are under stimulation almost as though for a corresponding time the stem were at rest. But these sides remain under stimulation for less than the presentation time and so the excitation does not suffice for the end reaction. When side *a* has passed into quadrant *C*

[1] It has been suggested that during the periods of no stimulation a counter-excitation is set up; but simple recovery from excitation seems sufficient to account for all the facts known. The process is apparently analogous to recovery from fatigue.

of its rotation and c into A, any residual excitation from the former position is balanced by excitation that would lead to a contrary reaction. All the while, therefore, the plant is under excitation, which is the greater the more opportunity there is for summation; and if the responses were not contrary the one to the other, curvature would show itself. The net result upon the rotated plant is that growth is at first accelerated as compared with a control plant rotated in the vertical plane; but long-continued rotation leads to fatigue and no response.

Position of equilibrium. — In order that a parallelotropic axis be in a position of stable equilibrium with respect to gravity, it must not only be parallel to its direction, but the stem must be erect and the root pointed downward. There is a polarity which must be conserved. Though the strictly inverted position for either roots or stems is one of little stimulation or possibly of none, it is a position of such instability that the slightest deviation leads to stimulation, which results in decided curvatures and recovery of the normal position. Much study has been given also to the position of maximum stimulation. The general results are most strongly in favor of a 90° deviation from the normal, as against 135° or any intermediate angle.

Variable intensity. — By comparing centrifugal acceleration with that due to gravity, it has been shown that it produces the same curvatures. So while it is not possible to alter appreciably the intensity of gravity, it is possible to vary this corresponding stimulus. Experiments in this line show that as the centrifugal acceleration is increased or diminished, the reaction time is shortened or lengthened, but whether proportionately or not is uncertain.

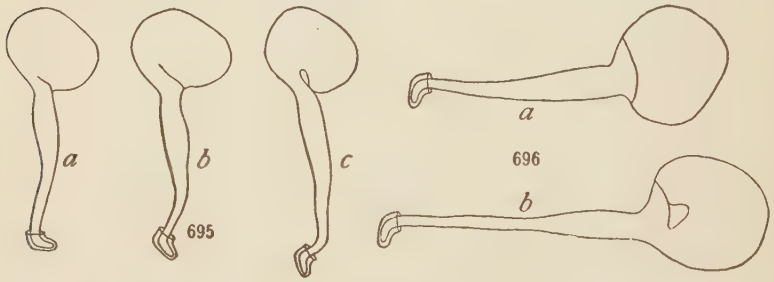
Thus, in earlier experiments with a root of *Vicia*, whose usual reaction time at 1 g[1] was 90–100 min., when the centri-acceleration was equal to 35–38 g, the reaction time was scarcely more than halved (45 min.); and when it was reduced to 0.001 g, the reaction time was barely quadrupled (6 hr.). In some late experiments, however, a root of *Vicia*, which reacted in 8 min. at 1 g, reacted in 0.25 min. with 27 g. Here the ratio is 32 : 27, a change in reaction time nearly proportionate to the change in stimulus.

Perceptive region. — It is extremely difficult to locate beyond question the exact region where the geotropic stimulus is perceived. In stems perception does not seem to be localized. If the statolith theory of geo-perception be true, it takes place probably in the starch sheath, a layer of cells around the vascular cylinder.

[1] 1 g = the normal acceleration due to gravity.

The most thorough experiments, however, have been made upon roots, and these seem to show that perception takes place mainly in the very tip, within a zone little more than a millimeter long, including the root cap. Indeed, the inner portions of the root cap itself are believed to be the cells most concerned. But the results also show that the growing region has some perceptivity.

This conclusion rests upon evidence derived mainly from three modes of experimentation: (*a*) *Decapitation.* Cutting off the terminal millimeter or two leaves the root still capable of weak response, after recovery from the shock. (*b*) *Mechanical deformation.* If root tips are made to grow into glass slippers (figs. 695, 696), or against a glass plate, so that the terminal millimeter is bent at right angles to



FIGS. 695, 696. — Roots of *Vicia Faba* with tips in glass slippers: 695, *a*, *b*, *c*, three stages in the curvature of the same root, 0 to 20 hours; 696, *a*, *b*, two stages of the same root; *b*, 18 hours after being placed in position *a*. — After CZAPEK.

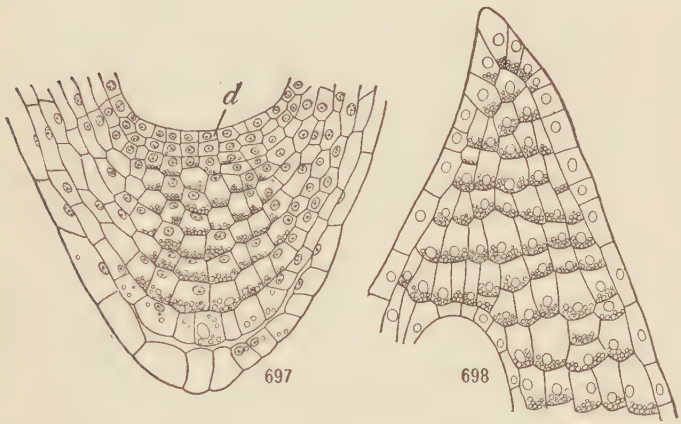
the body of the root and therefore can be placed in the position of stimulation while the rest is not (or *vice versa*), responses show the dominance of the excitation at the tip over that in the growing region; but the conclusion that the tip alone is perceptive is not warranted. (*c*) *Rotation.* Experiments in which the roots are fixed on a centrifuge, deviating 135° from their normal position, permit responses to be varied at will, according to the extent of the root tip beyond the axis of rotation. In all cases, if the stimulus to the growing region is to determine the response, it must be several times greater than is needed at the tip. Anatomical facts, in connection with the statolith theory of geoperception, support the physiological evidence above cited (fig. 697).

Statolith theory. — In its original form this theory was purely speculative. It postulated in the protoplasts of perceptive cells minute vacuoles, beyond the limits of microscopic vision, filled with a fluid in which there lay granules of slightly greater specific gravity, that would fall to the bottom of the vacuole, whatever position it occupied, and rest against the cytoplasmic membrane bounding it. In the normal position of parallelotropic organs this would lead to no excitation; but if the cells

were displaced, the granules would settle upon a new and excitable side of the vacuole wall, starting into action the mechanism of the end response.

There are many objections to this form of the theory, which was suggested by the visible otocysts of Crustacea, and the appearance of the centrosomes, which were then supposed to be common in the cells of seed plants.

In a more concrete form the theory has much to commend it, though it cannot yet be considered as firmly established. In this form no invisible structures are predicated, but the principle is the same. Certain



FIGS. 697, 698. — Perceptive regions: 697, median longitudinal section of the rootcap of *Roripa amphibia*; *d*, dermatogen; 698, apex of the coleoptile of the plumule of *Panicum miliaceum*. — After NĚMEC.

cells, notably those of the inner median portions of the root cap (fig. 697), the tip of the coleoptile in grasses (fig. 698), and a layer around the vascular cylinder in stems, contain rather large starch grains in such abundance as to attract attention. Moreover, these starch grains are freely movable, and in whatever position the organ rests, they accumulate on the physically lower side of the cells. They seemed to answer the requirement for bodies heavier than the fluid in which they lie, and therefore capable of setting up an excitation by coming to rest upon a part of the protoplast unaccustomed to their contact. It is assumed that certain areas of the protoplast are properly sensitive; that their excitation will start into activity the mechanism of curvature, which will eventually restore the organ to its normal position and so remove the irritating starch

grains from excitable areas, tumbling them again upon the side corresponding to the position of equilibrium.

These mobile grains are called statoliths and the cells containing them statocysts, after the analogy of the otocysts of the Crustacea, once thought to be organs of hearing, but now recognized as organs of equilibrium. The semicircular canals of the ear of vertebrates, with their fluid and mineral granules, have a similar function, giving the animal a sense of position or equilibrium.

Extensive anatomical studies have shown a remarkable parallelism between the presence of such grains and geotropic sensitiveness. Almost without exception, geotropic organs have mobile starch grains, while non-geotropic organs lack them. Moreover, when an organ, placed under unfavorable conditions (*e.g.* low temperature), has lost its mobile starch, it seems at the same time to have lost its geotropism, which is regained simultaneously with the rebuilding of the starch grains and not until then, although conditions favorable for response (had perception been possible) may have existed for much longer than the usual reaction time. This method of experimentation is, indeed, open to some objections; but the most serious one, namely, that the unfavorable temperature which determines the removal of the starch at the same time suppresses the geotropic irritability, is largely obviated by the fact that perception and the end reaction can be separately interfered with. Thus, by a temporary reduction of temperature, perception is not interfered with, for upon again raising the temperature with no further stimulation the end reaction proceeds as usual. Further, it is executed more promptly after the restoration of favorable temperature than it is when the low temperature is first used to eliminate the starch, and then at a favorable temperature stimulation is attempted. This indicates that the failure to obtain the curvature when there is no mobile starch is due to an interference with the mechanism of perception rather than with the mechanism of transmission or of growth.

Plagiotropic organs. — The erect position of certain organs is not necessarily determined by gravity alone, but may be due to the cooperative action of other stimuli. In like manner the oblique or horizontal position may be determined wholly by a response to gravity, or by some other single stimulus, or by simultaneously acting stimuli. Experiment alone can determine the agents in each case. Among plagiotropic organs which owe their position to gravity, some rhizomes that run horizontally beneath the surface of the ground are noteworthy. When such a rootstock is displaced by directing the tip obliquely upward or downward, curvatures ensue, precisely as in the case of parallelotropic roots, though, of course, the growth is much slower. This mode of reaction is known as *transverse geotropism* or *diageotropism*, corresponding to the positive and negative geotropism of parallelotropic organs. Quite similar behavior is to be seen in some peduncles, which are pendulous while the flower is in bud, but become in bloom horizontal, and in fruit

erect (figs. 1195–1197). When the change of position can be shown to be due wholly to gravity, this indicates that the peduncle undergoes with age a change in its mode of response. Well-known examples are offered by the snowdrop and the wind flower. Less generally known are like changes in direction when certain stems, erect in the seedling stage, develop into horizontal rhizomes in an older stage.

Diageotropism. — Diageotropism of a somewhat modified type is seen in the branches of the primary roots of some plants. These grow out at a definite angle, and, if displaced, they will curve until the normal angle is again attained. Similarly the oblique branches of trees sometimes are decidedly geotropic, and even the pendent ones may show it. Only by the most cautious and precise experimentation in each case can it be ascertained whether the positions assumed are due to gravity. Unwarranted generalizations in this direction are particularly seductive. In far the greater number of cases the position of organs is determined by a complex of stimuli most difficult of analysis.

Twiners. — Among the most interesting of the complex phenomena are those exhibited by twining plants, in which geotropic reaction of a peculiar kind plays a most important part. Twiners have slender stems with a very long growing region, and a tardy development of the lateral organs (leaves and branches), so that the long tips often look quite naked. These ends seem to travel in a spiral fashion around some suitable, slender support, and the mature plant is thus wound around it and clasps it tightly. At the outset the seedling, say of a morning glory, grows quite erect, and seems like a parallelotropic plant, as, indeed, a study of its reactions with a clinostat shows it to be at this period. After reaching a certain height the tip no longer grows erect, but declines to one side, and then a movement begins, quite like the irregular nutation that every erect plant makes, except that it is regular and more striking. The tip, standing in a nearly horizontal line, swings steadily around and is directed successively to every point of the compass. This may bring it into contact with a suitable support, around which it then proceeds to twine, the free tip continuing the swinging movement from the point of contact with the support. The fundamental feature of the twining, therefore, is the swinging motion.

Lateral geotropism. — Since the swinging movement does not continue when a twiner is properly rotated on a clinostat, it must be considered a response to gravity. As growth that can swing the tip sidewise can be effective only if it takes place on the flank, the inference is made

that the stimulus, instead of finally affecting the side of the stem next the earth, as it does in the younger stages of development, now affects the flank, determining there more rapid growth. According as the right flank or the left grows faster, the tip will be swung like the hands of a clock or in the opposite direction. The twining may then be designated as clockwise or counter-clockwise (see Part III, fig. 957). There is no fundamental reason, apparently, for one direction rather than the other. While usually the same species of plant twines always in the same fashion, closely allied species will differ in this; there are some species that twine indifferently in either direction; and there are a few in which the individual plant may change the direction of twining in the course of its development.

Rotation and revolution. — When growth of a given flank has swung the free tip around, this very act, by twisting the stem on its own axis, brings a new segment of the stem into the flank position and so exposes it to excitation.

This may be understood by representing the stem by a hexagonal pencil. If the side on which the name is stamped face the right with the pencil horizontal and the point away from the body, then this right flank may be imagined to be the one whose growth is accelerated; by that the point would be swung to the left, and by the time it has passed over 90° the pencil would be rotated on its axis through 90°, so that the stamped side would now face upward and the angle that was first at the bottom would now be the flank. This rotation may be imitated, if it cannot be seen to be a mechanical necessity when a horizontal portion of an erect stem is so rotated, by sticking the end of a pencil into a piece of rubber tubing just stiff enough to bend into a quadrant under its weight. Now upon swinging this apparatus without torsion, as can be done by holding the end of the tube and pushing the test pencil around with another, the rotation will become at once evident, being complete when one revolution is completed.

The new flank thus brought under the influence of gravity has its rate of growth increased, which swings the tip further, rotates the free part of the axis, and so brings another segment into the flank position. Given the sensitiveness of the flank to gravity, the revolving movement follows as a necessity.

The support. — When a stem is swinging thus, if it come into contact with some obstacle near the tip, flexure may carry it past the object; but if it strikes the obstruction further back, the bending may not be sufficient to carry the axis past the obstacle, particularly if it be of moderate size. Instead, curvature will soon occur in the part projecting beyond it, and the revolving movement will be continued by the apical

portion, which steadily wraps itself around the support. In the nature of the case it is not possible for twiners to wrap about large supports, nor those that are too nearly horizontal. Plants differ much in their capacity in these two points, a difference which depends chiefly upon the relative length of the growing portion of their stems, and consequently upon the precise distance of the most actively growing region from the apex. Few twiners encircle supports more than 15 cm. in diameter, or those that lie nearer the level than 45°.

Straightening. — The coils that a twiner forms at first are loose and of low inclination. Later they become steeper and hug the support tightly. This seems to be due to a return, in the last stages of growth, to the apogeotropism that they possessed in the seedling period, so that the stem starts to erect itself, with the effect stated. Very commonly the surface of the stem is rough, being ridged or angled or furnished with stiff hairs, which prevents slipping from a support too easily or sliding along it. Inspection of the stem in the regions no longer growing shows that it is twisted, the longitudinal ridges coursing spirally around the axis in a direction the reverse of the twining. This torsion is mainly the result of the final erection of the stem, though other causes cooperate to increase or diminish it.

This also is a mechanical necessity of the behavior. It can be imitated by coiling a long piece of rubber tubing on a table, marking a crayon line along the upper surface, and then lifting the inner end of the coil while the other end is held on the table, both ends being prevented from twisting in the fingers. Then it will be seen that the line apparently passes spirally around the tube, because the latter is twisted by the steepening of its coils.

The tardy development of the leaves and branches is very evidently an advantage in twining, for they would greatly impede the revolving movement and the subsequent tightening of the coils. When the branches do develop, they show the same behavior as the main axis.

This explanation of twining is not wholly satisfactory, because there are details of the process, and some features that appear only under experiment, that are not clearly accounted for; but it is far the best of the many theories that have been proposed, and in the major outlines that have been presented here it is certainly correct.

(2) THIGMOTROPISM

Tendrils. — Many plants are sensitive to mechanical stimuli such as contact or friction, as shown by the alterations of the rate of growth that lead to curvature. This phenomenon is *thigmotropism*. The

tendrils of climbing plants exhibit the most remarkable sensitiveness to mechanical stimuli, and it is by this means that their attachment to supports is secured. Tendrils are slender, even threadlike, lateral organs, branched or not, sometimes occupying the usual place of a branch, sometimes that of a leaf or of one or more leaflets of a compound leaf. They are therefore formed successively with the development of the main axis and its chief branches, so that the plant is constantly laying hold of a support by younger and younger tendrils. It may thus climb to great heights, while the main axes remain very slender and wholly unable to support their own weight, much less that of foliage, flowers, and fruit. The most important feature of the tendril is its irritability to contact, and the curvatures which follow as end reactions.

Behavior. — When a tendril is young and only about one fourth grown, it may be either straight or curled up into a loose spiral, of which the convex surface corresponds to the under side. If coiled, it unrolls as its period of rapid growth begins, at which time also begin nutating movements that are almost as regular as the revolving movements just described in the twiners. These tendril movements, however, are not due to any known external stimulus, but must be called at present autonomic. The tip is thereby swung in all directions and is thus likely to come into contact with some suitable support. When it does so, it quickly wraps around it. After a time, through continued and unequal growth in length, spiral coils appear in the region between the axis and the attached part, increase in number and closeness, and become more and more firm, until this part has become a veritable spiral spring by which the plant is slung to its support. These results are attained in the following way:

Stimulus: friction. — The tendril is sensitive to contact, usually throughout its whole length, and on all sides, but most so towards the tip. Yet it is not sensitive to contact in the narrow sense; it is because things come into contact with the tendril in more than one place when they touch, so that it is only by multiple and successive contacts, and usually by shifting contact or friction, that the tendril is excited. Liquids (even the heaviest, mercury), if entirely free from solid particles, and perfectly smooth solids, like gelatin, do not produce excitation. Rain, therefore, does not cause useless movements of tendrils. But very slight rubbing movements of excessively light objects suffice to start them. It has been found, for example, that a bit of thread, weighing by estimate only 0.00025 mg., if moved by the wind over a very sensitive tendril, will induce curvature.

While the tendril may be sensitive throughout, the responses evoked by excitation differ sometimes according to the region stimulated. Thus, a stimulus applied to the "under" side, which at the time of greatest sensitiveness has usually grown near the apex a little less than the other, so that at the tip it is slightly concave, results in a curvature. So also does stimulation of the flanks, and in some tendrils that of the upper side too. But there are some others which give no sign if rubbed on the upper side, except that stimulation there will inhibit a simultaneous stimulation on the under side, which ordinarily would result in a curvature.

Primary response. — The first result of slight rubbing contact with a suitable support (that is, one that is small enough for the tendril to encircle, no matter in what position it stands) is a prompt curvature. In sensitive tendrils under favorable conditions this follows in the course of a few seconds (5–30), but in others in a few minutes. The facts observed are that the cells on the convex side become suddenly considerably elongated, while those on the concave side become somewhat shortened. This and the promptness of the end reaction suggest a turgor change, and many observers have concluded that such is the mechanism of the primary curvature, and that it becomes fixed later by growth. Others attribute these results to a very rapid and extraordinarily sudden growth of the cells of the convex side, and to the consequent compression of those on the concave side. It is not improbable that the truth in this, as in many similar recondite and much controverted matters, will prove to lie between the contentions. So it may very well be that a turgor variation begins the movement, whereupon growth follows it up more promptly than usual, and extends and completes the encircling of the support.

Secondary response. — After the tendril has become firmly attached, the excitation extends toward the base of the tendril, producing an inequality of growth on the opposite sides (in this case the "upper" side becomes the convex one) that throws this part of the tendril into coils (see Part III, fig. 958).

This coiling may be rudely but essentially imitated by placing in a pan of water a narrow strip, slit from the scape of a fruiting dandelion which has not attained its full height, and by pinching each end in a short folded piece of sheet lead to prevent twisting. After a few hours the strip will be found coiled into a spiral, with one or more reversals of direction just as in the tendril, though more irregularly. Here the tissue next the pith cavity grows and becomes more turgid than the epidermal and cortical tissues. The reversal of coil is a mechanical necessity if the ends are not free to rotate.

These coils are not merely the result of continued growth of the tendril; for if one not full grown becomes attached, it does not reach its possible

maximum length, but from that time grows only in such a way as to throw it into the spiral coils. One which does not become attached grows longer and longer, but finally shrivels, usually without coiling. Sooner or later, upon the cessation of this second phase of growth, the phase of maturation is marked by the development of mechanical tissues, which add strength to the elastic coils. The nature of the stimulus that brings about the final coiling is uncertain. It may be the strain from the weight of the plant after becoming fastened, or the spreading stimulation from the contact pressure (for the attachment coils compress the support), or some unsuspected stimulus may be brought into action. There are many other stimuli which will evoke reactions from the tendrils, but none which in nature has any importance.

Sensitive petioles. — There are other plant organs that behave in a similar way to the tendrils, though none of them is so sensitive. The petioles of *Clematis* and of the climbing *Tropaeolum*, or "nasturtium," are familiar examples. While such petioles do not wrap themselves around the support nor form spiral coils as well as a tendril does, nevertheless they are efficient prehensile organs, enabling the plants to climb high.

Dodders. — Any account of twining and climbing plants would be incomplete without mention of the dodders (*Cuscuta*), leafless yellowish parasites that wind their stems around and clamber over erect herbaceous plants, sending haustoria into their stems, whence they obtain food and water. In the first stages of development, the species that have been studied germinate in the soil, and the young seedling behaves as a twiner; but shortly after it has found a suitable host and begun to twine around it, the lower part of the stem dies away, while the upper part continues its growth at the expense of the host. The further twining, however, instead of being dependent upon gravity, is the result of a contact stimulus like that which enables tendrils to secure a hold, so that the parasite enwraps supports in all sorts of positions. In the possession of these two modes of response at different periods of development, the dodders are unique (see further Part III, fig. 1081).

(3) Traumatropism

The wounding of plants produces immediate reactions, mostly invisible, but root tips may be so wounded as to lead to curvature. If an active tip be branded on one side with a hot iron or glass rod, or if it be similarly cut or otherwise injured, the tip will turn to one side. When the injury is severe, this may so seriously impair the tissues on the injured side that their growth will cease, and the injured side will become concave near the point of injury, because there the tissues shrivel and the growth of the other side goes on. This is not a true reaction, since the result is

due merely to mechanical interference with growth. On the other hand, if the injury is one that does not deeply involve the tissues of the injured side, a curvature will follow that turns the tip away from the injury. Here an excitation started by the wound has spread thence to the region of most rapid growth, inducing a true tropic curvature. After experiments by attaching bits of cinder, paper, and the like to root tips by means of gum, it was believed that the root tip, by its sensitiveness to contact, was a sort of directive organ, which could feel its way through the soil, and avoid injury. But in these experiments the gum injured the cells, and it, not the attached particle, was the stimulating agent, so that the response was actually to injury and not to contact. It is not probable that sensitiveness to injury is of any advantage to the plant, as it undoubtedly is to a conscious organism. Occasionally, of course, traumatropism might be advantageous to a plant in getting a root tip once injured out of immediate danger of further injury.

(4) Rheotropism

Roots grown in a current of water of adequate velocity may respond by directing their tips against the current. In this case the stimulus might be the strains set up by the pressure of the current, or the impact and friction of the water particles against the surface. Its precise nature is not satisfactorily determined, but it seems to be the pressure of the water and the resulting strains rather than mere contact or impact. The whole of the growing region seems to be sensitive, and not the tip alone. It is not apparent that this reaction can have any significance for the plant in nature.

(5) Chemotropism

Of fungi. — Chemical compounds may not only be usable in repair and constructive work, but may so affect the living substance and its chemism as to act upon it as stimuli. Since by diffusion they may act from one side, these stimuli may be directive, causing curvatures toward or away from the source, which are manifestations of chemotropism. Very striking reactions to chemical compounds of many sorts have been ascribed to the hyphae of fungi and to pollen tubes. Chemotropism of the latter may be maintained still, as it has not been seriously impeached; but that of fungus hyphae has been brought under suspicion by the latest researches, and may be either established or disproved by further study. For the hyphae to be sensitive, especially to carbohydrate and other foods, would be of much service in inducing them to grow in directions that would bring them into favorable feeding regions, and precisely this power has been ascribed to them. For instance, when certain fungus spores are sown in a layer of gelatin containing no nutritive materials, between layers of gelatin, on the one side with nutritive material and on the other side without, it is reported that the hyphae turn toward the layer of nutritive gelatin. The same reaction was found to

occur when the central layer contained food, provided the outer layer had enough more of the same to act as a stimulus. (In this case the ratio had to be about 10 : 1. See Weber's law, p. 448.) Likewise the hyphae grew through fine perforations in thin plates of mica or celluloid, when the nutritive gelatin was thus separated from the other, suggesting the way in which fungus hyphae, arising from spores on a leaf, turn into a stoma and so find their way into the interior of a leaf of their host. In fact, when leaves were injected with a solution of food, like sugar, fungus hyphae of many kinds are reported to turn into the stomata, though they do not naturally grow on the leaves used. A great variety of substances were tested in similar ways. Some proved to be attractive, some repellent; and the reaction varied according to the concentration of the solute, though generally the hyphae were injured before the limits of concentration for repelling effects had been reached.

On the other hand, an apparently careful repetition of many of these experiments gave negative results, in that the numbers of hyphae reacting positively is so slightly in excess of the number indifferent or negative, that the results seem scarcely more than chance, or ascribable to other than the cause assigned heretofore. A complete restudy of the matter will be necessary.

Of pollen tubes. — When pollen tubes are developed under a cover glass in company with a bit of the stigma of the same plant, they turn toward it, from whatever direction they first issue. An ovule or a bit of the wall of the ovary is likewise attractive. Investigation shows that soluble carbohydrates and proteins are here the attractive substances. It seems likely, therefore, that the growth of the pollen tube toward the ovules is directed by the diffusion of such substances, which are always found in these organs. (See the chemotaxy of sperms, p. 448.)

Aerotropism. — A special form of chemotropism has been called *aerotropism*, and was first ascribed to roots. When certain gases, especially oxygen, diffuse against young roots from one side, it is reported that the root curves toward the source of the gas. These results also have fallen under suspicion. Recent investigations are conflicting; and one is left in some doubt whether to ascribe the curvatures to a true reaction to gases, in accordance with the weight of evidence, or to moisture, in which case they belong to the following special category of chemotropic response.

Stems also have shown sensitiveness to O_2 and CO_2, and it may be that aerotropism is more general than has heretofore appeared. It is not evident that it can be of any great advantage to either roots or stems, except, perhaps, those of swamp plants.

Hydrotropism. — Another special form of chemotropism, which has been named hydrotropism, designates the sensitiveness of roots, the hyphae of some fungi, the rhizoids of liverworts, etc., exhibited by turning toward or away from the source of diffusing water vapor, or capillary water in soils. When seedlings are grown in an atmosphere less than saturated with water vapor, so that the roots, as they grow, pass further and further away from a wet surface,[1] it will be found that they deviate presently from the perpendicular, inclining toward the wet surface; soon again they turn downwards, but once more return to the moisture, and this may be repeated many times. Plainly the roots are subject here to two stimuli acting nearly at right angles, gravity and the diffusing vapor. First the one dominates and then the other. Were it not for the long reaction times the root might be expected to take an intermediate direction, the resultant of the effects of the two stimuli; but as in the case of geotropism alone (see p. 460), the after-effects carry the root tip past the position of equilibrium, whereupon the other stimulus gives it such strong and long excitation that its after-effects carry the root again past the equilibrium point; then the gravity stimulus comes upon it again; and so it weaves back and forth.

The vegetative hyphae of the mold fungi may show positive hydrotropism and their sporangiophores negative hydrotropism. It can easily be shown that the rhizoids of *Marchantia*, which normally grow straight downward, will deviate toward a moist surface in the same way as roots; only the moisture stimulus is dominant over gravity. Roots in the soils also grow towards the moister regions, and especially do they tend toward tile drains, into which they may penetrate, often branching profusely enough to plug up the drain completely. Part of this directive effect may be due, and probably most of the branching is due,[2] to chemical stimulation by the solutes.

(6) Phototropism

Stimulus. — Of all the external conditions that act upon plants, light is one of the most variable, for from time to time it differs in direction, in intensity, and in quality. Quite apart from its fundamental relation to all life in furnishing the energy for food making, are its effects as a stimulus. Whereas the most effective quality of light for food making

[1] As by planting them in coarse sawdust held in place on the under surface of an inclined board by bobbinet.

[2] In which case this is a morphogenic effect. See p. 435.

is the red-yellow, the most effective light as a stimulus is that near the violet end of the spectrum. Since this is the region of least energy, the shortness and frequency of the waves are the important features of light as a stimulus. In this respect the red end of the spectrum, though its energy is far greater, behaves as darkness.

Response. — In general the response of plants to light differs according to the usual attitude of the organ and its mode of growth, for which indeed light is largely determinative. Parallelotropic organs respond by directing their tips toward or away from the source of light, while plagiotropic organs place themselves more or less at right angles to the direction of the rays. Primary stems, therefore, are mostly positively phototropic, and some roots, particularly aerial roots, are negatively phototropic; while leaves are mostly transversely phototropic or diaphototropic.

These phenomena were first known as heliotropism, etc., and are often still so called, because the sun in nature is the source of all light. It seems better, however, to use the wider term, since plants respond in the same way to artificial light, which is so largely used in experimental work. The general result of these reactions is the same as of those to gravity, so far as the same organs are sensitive to both stimuli, though the two act from opposite directions in nature.

Intensity. — The intensity of the light may determine either a positive or a negative curvature, and within certain limits between these two there is a range of intensity which calls forth no visible reaction; this is the point of phototropic indifference. It is by no means the point of no excitation. At high intensities that call forth negative curvature, injury soon appears. Near the lower limit of intensity that can produce an end reaction, plants show themselves very sensitive to light. Thus, radish seedlings respond to the light of a single candle at a distance of about 8 m., the broad bean (*Vicia Faba*) at 22 m., and a cress (*Lepidium sativum*) at about 55 m. The differences that plants can distinguish are within the limits of error for the unaided eye, and are not very easily distinguishable even with the photometer.

Time relations. — The presentation time, of course, depends upon the intensity of light used, and is approximately inversely proportional to it. The greatest range of presentation time recorded is that for etiolated seedlings of oats, being 0.001 second with light intensity of 26,520 Hefner candles, and 13 hours with light intensity of 0.000439 Hefner candle. Intermediate light intensities give corresponding inverse proportional intermediate presentation times. As a rule the younger an organ is, the

more sensitive it is; but this is by no means universally true. The reaction time varies from a few minutes to some hours, depending upon the temperature, the intensity of the light, and the general condition of the plant.

Reversal. — The reactions to light also are often reversed with age. This is especially seen in flower stalks, which at the time of blooming are likely to be positively phototropic, but later, during the ripening of the fruit, many become negatively phototropic, carrying the fruit under the leaves or even into crevices of the soil or rocks on which the species grows.

Mechanism. — The mechanism of the response is the same as in geotropism, and occurs in the same region; namely, that of most active growth, where one side grows more rapidly than the other, leading to a curvature whose tendency is to direct the axis into the line of the light rays. This inequality of growth is brought about by its acceleration on the convex side and by simultaneous retardation on the concave side. These changes in rate are not due to the fact that the rate of growth is retarded by light (see p. 435), for this (apparently applicable to positive phototropism and once an accepted explanation) could not account for the acceleration on the convex side, nor for any of the changes in negative phototropism. The reaction is determined by the mechanism of the parts concerned and not by the *direct* influence of the stimulus.

Perceptive region. — In many phototropic reactions there is a distinct perceptive region, a propagation of the excitation, and an end reaction in a different region. Thus when seedlings of millet raised in the dark are exposed to lateral illumination, the sharp curvature that presently appears in the axis ("hypocotyl"), which is rapidly growing, can be shown by appropriate shading to owe its origin to the stimulus perceived by the leaf at the tip ("cotyledon") and not to excitation of the axis itself. In a similar way the seedlings of oats show that though the whole of the subaerial part is sensitive to light, the tip is much the most so, and that excitation, spreading thence downward, dominates even contrary excitation set up in the lower parts.

What is perceived? — Nothing is known as to the mode of perception or the structure of the perceptive organ. Indeed, it is not entirely certain what sort of stimulus the plants perceive; whether it is the direction of the rays, that is, the line of propagation of the waves, or whether it is inequality of the illumination of different sides. It has even been suggested, in casting about for something tangible, that plants distinguish between the different pressures in the lighted and shaded portions!

It has been shown that the impact of the ether waves of full sunlight produces a pressure equal to about half a milligram per square meter. In a seedling of oats at this rate the plant would have to be sensitive to a difference of five millionths of a milligram and probably to one tenth of this infinitesimal amount. This is simply inconceivable!

It seems most likely that it is the difference in the lighting that is perceived, for the intensity of the stimulus has an important bearing on the form of the reaction, and plants are able to respond to differences of illumination coming from different sides that are too small for the eye to distinguish.

Plagiotropic organs. — The behavior of plagiotropic organs toward light is especially interesting, because it seems to be usually of the very greatest importance for the welfare of the plant in food making by leaves, thalli, etc. The fact that the leaves of most common plants, set before a window, place themselves at right angles to the incident light, attracts attention at once. If the pots be turned around, the position of the leaf blades will soon be changed, and they face the window again. Thus the leaves obviously come into a position most advantageous for receiving the maximum of energy for photosynthesis. The corresponding orientation in the open shows that it is not the direct sunlight alone to which the leaves respond, but rather what may be distinguished as sky light; that is, the brightest diffused or reflected light. Indeed in some cases the direct sunlight is evidently too intense, and the plane of the blades is set at an angle to the direct light, the edge in some plants being directed upward.

Compass plants. — When the position of leaves is uniform or nearly so, and corresponds approximately with the plane of the principal meridian, the plants are known as compass plants. The wild lettuce, *Lactuca Scariola*, is the most widely distributed of these, and on the prairies and along railways, the compass plant, *Silphium laciniatum*, which illustrates the habit far better, is common. Other plants in this and other countries have the same habit. That this is a response to intense light is seen easily in the lettuce, for when this plant grows in the shade, its meridional position is not assumed.

Fixed light position. — The reaction of a leaf to light can occur only while it (especially the petiole, which is the seat of most curvatures) is still growing or capable of growing. During this period the habitual responses lead finally to a position known as the fixed light position, a sort of resultant, which on the whole gives the blade the most advantageous illumination. One result of this is the arrangement of blades in such a way as to avoid shading one another. This produces the so-called leaf mosaics (see Part III, p. 543.) The movements of the leaf

in attaining these positions may involve curvature, lengthening, and twisting of the petiole and even of the blade itself.

Perceptive region. — Perception in most cases seems to occur in the blade, whence the excitation is propagated to the petiole, whose upper parts grow for the longest time, and even after elongation has ceased may be started into growth again by the light. In some cases, however, the petiole itself may be sensitive to light, and may either cooperate with the blade, or alone be responsible for both perception and curvature.

The mechanism of perception has been sought in the epidermis of the blades. It has been found in some cases that the epidermal cells are domed and that they act as lenses (fig. 699), focusing the light upon the lower side of the cell, so that a spot in the center is much more brightly illuminated when the light strikes at right angles. The position of this area is shifted when the leaf blade is oblique to the rays. Correspondingly, it is assumed that the protoplast is excited when the bright spot rests on any but the central area. There is no doubt that the structures described concentrate the light, for that can be shown photographically; but there are sensitive blades in which domed epidermal cells are wanting, and experiments do not yet unequivocally sustain the assumed distribution of irritability. The perceptive organs of leaves have not been located other than by this still doubtful hypothesis.

FIG. 600. — Ordinary epidermis and "ocella" (*o*) of leaf of *Dioscorea*. — After HABERLANDT.

(7) Other tropisms with radiant energy

Electrotropism. — Currents of electricity passing through the medium in which plants are growing, and presumably through the organs themselves, evoke various curvatures according to the density of the currents used. By nature roots lend themselves especially well to experiment. Some of these responses, and possibly all of them, are due to one-sided injury of the roots. The effects appear to be due to electrolysis of the solutions used; but whether by the direct action of the ions outside or by the withdrawal of ions from the protoplast is not certain. Electrotropism or galvanotropism may therefore be hardly more than a special form of chemotropism. It does not seem likely that such stimuli act to any important extent in nature. The more important effects of galvanic and static currents upon development have already been described (see p. 438).

Thermotropism. — Thermotropism is also of little importance. Both roots and stems of particular plants turn toward or away from a blackened plate radiating heat, according to the temperature. In a similar way roots growing in sawdust will grow toward or away from a source of conducted heat. Neither form of reaction can be of much importance in nature.

The same may be said of reactions to radium and its salts, as well as those to X-rays. The injurious effects of these are more pronounced than the tropisms.

8. THE DEATH OF PLANTS

The cycle ends. — From the foregoing it has become evident that the growth and development of plants does not proceed uniformly, but that it is profoundly influenced — one may even say controlled — by external conditions; and since many of these external conditions evince a decided periodicity, growth and development exhibit a corresponding periodicity. But it has also become apparent that growth and development are likewise affected, and in many particulars as profoundly affected or controlled, by factors that are wholly internal, so far as is known at present. It is found, further, that these factors may give rise to periodicity in growth and development; for, however uniform the external conditions may be, neither proceeds uniformly. In nothing is this more impressively shown than in the fact that the cycle of development, in spite of all that can be done, sooner or later comes to an end, and the plant perishes, leaving behind comparatively few living cells, if indeed it leaves any, out of the unnumbered millions that may have constituted its body.

No inherent reason for death. — There does not seem to be any inherent reason why a plant should die. The material of which it is composed is all the while undergoing decomposition and repair. In a perennial plant, like a tree, the tissues in great part are renewed annually, so that though the living and the dead stand together as a sort of unity, which may have occupied the place for centuries, the oldest of the living parts is only a minute fraction of these centuries old. In such a plant, however, it becomes increasingly difficult to supply the extremities with the needful materials, because they are steadily becoming separated by greater and greater distances. The leaves are yearly further from the ports of entry for water, and the roots are yearly further from the source of food. With expanse of branching, mechanical overthrow threatens more and more. Thus the physical conditions are steadily becoming more severe, and it is easy to imagine why the plant must finally succumb. Yet the long persistence, even after it has become evident that a tree has reached the practical limit of growth, shows that there is nothing in the living parts themselves which determines the end; and still more is this shown by the fact that cuttings may be taken from an old tree and successfully started upon a new cycle which may be as long as the parent's. Thus, the Washington elm at Cambridge has been struggling against adversity for more than a quarter of a century, slowly

succumbing in a losing fight; but a cutting from it is now a thrifty, well-grown tree on the Boston Common.

Reproduction. — In the smaller plants the inception of unfavorable conditions is often a signal for the gathering together of all the living material into a form that can endure adversity, as with the encystment in bacteria, fungi, and algae. Under these circumstances also the protoplasm is divided into several or many parts, each appropriately protected; thus multiplication becomes possible if more than one part escapes injury and finds suitable conditions again for development (see *Botrydium*, p. 33, and many other illustrations in Part I). This simple situation has been worked out, in the higher plants, into elaborate mechanisms of reproduction, which are now not always obviously related to the inception of unfavorable conditions. Yet methods of cultivation indicate that the formation of spores, even in the seed plants, in which naturally it often far precedes the period of flowering, may be initiated by conditions unfavorable for vegetative growth. Until these conditions can be more exactly designated and analyzed, it is unprofitable to consider them more in detail. At present, then, all that can be said is that unfavorable conditions bring about a redistribution of the living material, of which as much as possible resists and persists. Thus, since the beginning of things, we assume, there has been an unbroken chain of living matter, shaping itself for a time into organisms more or less complex, and then retiring into the simplest and least exposed forms, to begin another cycle of development when the conjunction of internal and external forces permitted.

What is death? — The abandonment by the living protoplasm of a body previously constructed, or the destruction of the protoplasm wholly or in great part, is what is usually meant by the death of a plant. Since plants conspicuously lack individuality whenever they become more complex than a single cell, the severance of a plant, even the highest, into two or more parts may not bring death, as it does to so many of the higher animals, but rather renewed vigor. Correspondingly, the death of even a large part of the body does not necessarily bring death to the whole, but often likewise renewed vigor to the parts that persist.

Local and general death. — Extensive local death, as this may be called for convenience, is possible in plants without the serious consequences that follow in the higher animals, first because plants have so little specialization of organs and so many of the same kind; second, because they have no circulatory system that might rapidly distribute to other parts

deleterious substances arising in the dead region, and so cause their injury or death; and third, because they have no nervous system, putting into quick communication sound distant organs with hurtful stimuli from the dead ones. Yet these differences, on the surface so marked, are in reality not fundamental, for what is general death in the animal is in reality only an extension of local death to the several tissues and organs more rapidly than in plants. But each part dies at its own rate and only because the interruption of the activity of one organ has created conditions unfavorable to the other.

Irreversible reaction. — The phenomena of death are not easily described. Certain changes in the appearance of the cytoplasm are visible under the microscope (such as are familiar in fixed cells and are too commonly thought of as the normal appearance of cytoplasm), chiefly aggregation and vacuolation; but the significance of these is not known. Alteration in the chemical processes and different behavior, especially permanent insensitiveness to external stimuli, are the most important marks of death. During life the protoplasm is constantly adjusting itself to new conditions, each response suited to the stimulus, whether in a favorable or unfavorable direction. These responses of normal life are assumed to be reversible, as are many chemical reactions. But when the responses to severe stimuli become irreversible in too great measure, the possibility of readjustment to new stimuli is past; this condition is death.

Diseases. — Plants are often killed by diseases which may arise from the disturbance of function wrought by external agents, such as the elements of climate, the solutes of the soil, gases in the air, etc. Or disease may be due to the invasion of the body by parasites, which rob the host of food, interfere with its water supply, or upset some necessary function. A study of diseases forms a great field in itself, *plant pathology*, under which name *therapeutics*, the study and application of remedial measures, is also usually comprehended. It is one of the divisions of botany which is of great economic importance, and one whose study has reached its highest level in this country, where the remedial and preventive measures devised save annually many millions of dollars. The knowledge of infectious diseases has been most extensively developed, but therein a great field for investigation still lies open, and a still greater one in the more difficult study of functional disorders.

Mechanical injury. — Mechanical injuries often lead to death, especially because they expose the plant to infection by bacteria and fungi.

Unwise pruning of trees in our cities, much more the heedless hacking at the hands of linemen stringing telegraph and telephone wires, and the gnawing by horses carelessly hitched to the trees, frequently open the way for infection by some deadly parasite. Ice storms, hail, winds, and lightning all contribute to serious mechanical injuries at times, whose direct effects are less to be feared than the indirect.

Heat and cold. — High temperature is a fruitful cause of local death, for this is often associated with a deficiency in the water supply. There has been recognized a falling of the leaves, especially of trees, in midsummer, which is due to the heat, and may amount to a large per cent of the total foliage. The older leaves, and those least favorably situated for receiving sufficient water (the latter are at the same time most exposed to the direct rays of the sun) are the ones that suffer most. Low temperatures kill tender plants by direct injury to the protoplasts, even before the freezing point is reached. Others are killed only by the freezing itself, probably because this withdraws water from the protoplast and vacuoles, thus concentrating the solutions, perhaps to a point where certain solutes may become poisonous. There are many plants, however, which are able to withstand freezing, and on gradual thawing the water is taken back into the protoplast again. All the trees and shrubs and the persistent parts of herbaceous perennials are liable to be solidly frozen, often more than once, in the winters of the northern states and Canada, but they usually bear this unharmed, though the trees then have almost a maximum water content. The most serious danger in the northern winters, especially to the evergreens, is that during a warm period the evaporation will surpass the income from the shaded and frozen soil.

Temperature and water. — In general the proportion of water present determines the resistance to injury by low and high temperatures, other things being equal. Thus air-dry seeds withstand the lowest temperature yet tried, that of liquid hydrogen (− 250° C.),[1] and germinate freely when planted; while the same seeds, if soaked in water until swollen, will be killed at a very much higher temperature. In like manner temperatures short of absolute charring are borne by dry seeds, while a few minutes' exposure at 70° C. will kill soaked ones. Similarly, plants of firm texture and little sap withstand unfavorable temperatures better than watery ones.

[1] Doubtless they will endure the temperature of liquid helium (probably within five or six degrees of the absolute zero, — 273°) if enough is ever obtained for such a test.

Poisons. — Various substances, comprehensively known as poisons, kill the protoplasts, when their concentration is sufficient. At lower concentrations many of the very same substances accelerate growth or development or special functions. The action of these substances may depend upon their dissociation in solution into ions, if they are electrolytes, or upon the molecules themselves, or both. Some act by coagulating the protoplasm and others induce changes of a different sort, not accurately known. Ionic hydrogen, silver, copper, and mercury are remarkably injurious. A solution of only one part per million of a silver salt is quickly fatal to the roots of lupines, and still less of mercury kills. Some very important economic measures depend upon the extreme sensitiveness of protoplasm to such substances. For microscopic study it makes possible the almost instant killing of the protoplasts, and by combining a fixing with the killing agent, the preserving of the protoplast in a form which approaches closely the condition in life; so far, at least, as can be judged from what can be seen of minute structures in the living condition. Further, the poisonous nature of such substances makes it possible to employ them against the agents of infectious diseases, particularly those that grow on the surface of the host. The poisons act at lower dilutions upon the parasite, because its protoplasm is more accessible than that of the host, whose epidermis prevents injury in great measure. The usual form in which they are employed is in solution, which can be sprayed at appropriate times over the host. Many most destructive diseases are thus held in check. Where a disease is transmitted with the seed, they may be disinfected by short soaking in a suitable solution, without materially injuring their germinative power. The modern methods of antiseptic surgery, personal and municipal hygiene, and the treatment of infectious diseases rest essentially upon like principles, for in nearly all these cases the organisms to be combatted are plants.

The death of plants appropriately terminates a discussion of their behavior.

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